THE EXTERNAL SURFACE OF *DICTYONELLA* AND OF OTHER PITTED BRACHIOPODS

by ANTHONY D. WRIGHT

Abstract. The external surface of *Dictyonella* is characterized by a smooth depressed umbonal region and a pitted ornament. The exposed part of the smooth plate, here termed the *colleplax*, is enlarged by resorption of the outer shell. A model is developed to explain the mode of function of the colleplax and its relationships to the soft tissue. The apparently complicated surface pattern of *Dictyonella* and other pitted brachiopods is shown to be produced by simple radial growth modified by various factors. The surface cells of *Dictyonella* may have up to nine puncta on the cell floor and variations in depth of the cells partly reflect preservation of the cavernous calcareous shell, which is apparently composed of a thin primary layer and a fibrous secondary layer. An Ordovician species, *D. planicola* sp. nov., possesses an ornament intermediate between typical Silurian *Dictyonella* and the presumed ancestral *Eichwaldia*. In other brachiopods, pitted surfaces may also be related to caeca, or to temporary marginal caeca in impunctate stocks. Those of other genera bear no relation to endopuncta and may be grouped as (*a*) complete or incomplete superficial pits possibly containing organic substances; (*b*) anteriorly directed shallow *aditicules* housing marginal setae; and (*c*) smaller and more steeply inclined *arrugiae* containing other sensory bristles.

James Hall described *Dictyonella* as 'one of the most interesting genera among the Brachiopoda' (1868, p. 227). Its calcareous valves are instantly recognizable by their attractive, net-like ornament; and as the genus is widely distributed in rocks of Silurian age, many workers have described and discussed its peculiarities following the earliest description of 'cette jolie espèce' as *Terebratula capewellii* by Davidson (1848, p. 327).

A feature recognized by Billings (1858) in establishing the genus *Eichwaldia* was that the 'large valve (is) perforated in the umbo for the passage of the peduncle (with) the place of the foramen beneath the beak occupied by an imperforate concave plate' (pp. 190–191), in addition to internal structures that were quite unlike any other known brachiopod. Thus the plate within the apical perforation of Billings is situated slightly below the surface of the pedicle valve (Pl. 62, figs. 1, 4), an aspect of the shell not recognized by Davidson either in his original description or in his 1869 description where his species is cited as *Eichwaldia*? *Capewellii* with an accompanying illustration (pl. 25, fig. 12) which shows the pitted ornament to cover the entire umbonal region. Davidson later recognized that the smooth triangular area was in fact present on the ventral umbones of all the specimens he had seen (1883, p. 141). Hall realized that the type species of *Eichwaldia*, the middle Ordovician *E. subtrigonalis* Billings, did not possess the distinctive net-like ornament of Silurian *Eichwaldia* species although it was closely similar in all other features. Accordingly Hall and Clarke (1894, p. 311) suggested that *Dictyonella*, a generic name Hall had intended using for his species *Atrypa coralifera* before *Eichwaldia* was erected (Hall 1868, p. 74), be used to accommodate the ornamented Silurian species. In the stratigraphic context it should be noted that genuine *Dictyonella* have now been recorded in rocks of Upper Ordovician age from several localities (Amsden 1974, p. 78; Wright 1974, p. 239), and the genus also ranges up into the Middle Devonian in eastern Kazakhstan (Kalpun 1967).

Only four brachiopod genera are known to possess the distinctive depressed, smooth umbonal region, but the character was regarded by Cooper (1956, p. 947) as meriting subordinal recognition. Despite wide consideration of the origin and affinities of these shells for over a century, their systematic position relative to other brachiopod stocks remains a mystery. The matter was discussed in the *Treatise*, where the suborder was placed with some uncertainty in the class Articulata by

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Rowell (1965*b*, p. H359); the subsequent study of the shell structure by Williams (1968*a*, p. 48) was inconclusive and could not confirm the questionable articulate affinities of the group. Wright (1979) accepted the Articulata as a valid class, but did not regard the inarticulates as forming a comparable cohesive entity and believed their disparate morphology and shell structure in particular to indicate several independent developments from already diversified infaunal phoronid-like lophophorate ancestors ('brachiophorates'). In the case of *Dictyonella* and its allies the migration on to the substrate and associated secretion of a calcareous shell would not have taken place until the Ordovician radiation (p. 248).

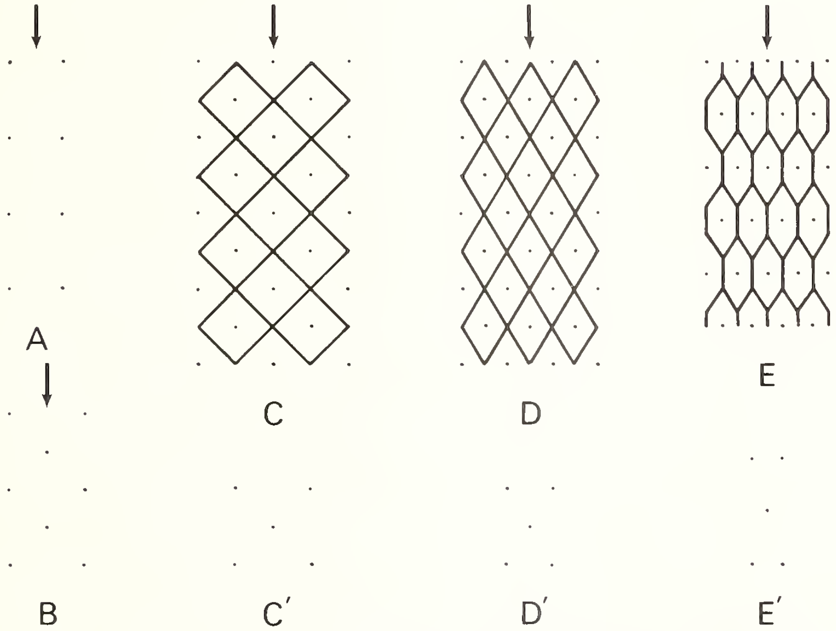
A pitted external surface is not the sole prerogative of *Dictyonella*, but is developed occasionally within a wide range of brachiopod orders. The appearance of the pits is by no means uniform, the common characteristic being that they are located and are visible on the outer surface of the shell. In many genera the pits are restricted to the external layers; in others, as in *Dictyonella*, they are associated with puncta produced by mantle caeca which penetrate the inner shell layers, and thus in the fossil are connected to pores opening on the inner shell surface. Among the chitinophosphatic brachiopods, the surface pitting occurs in the Paterinida and the Trematidae, and rarely in other genera such as the obolid *Glyptoglossella*. In the calcareous Orthida, a number of stocks, both punctate and impunctate, show surface pittings varying from scattered exopuncta to a regular net-like development. Surface pittings occur too, rarely, in the Pentamerida, Spiriferida, and Rhynchonellida. In the other major brachiopod groups, the Terebratulida and Strophomenida, it is not certain that this type of development has taken place. A specimen of a poorly known Recent terebratulide, *Surugathyris surugaensis* Yabe and Hatai which was figured by Hatai (1940, pl. 1, fig. 38) does show what may be exopuncta, but I am not aware of any other member of the order which develops surface pitting as opposed to the reticulate and sometimes spiny surface typically seen in *Dictyothyris*. Although the surface ornament of the strophomenides is unusually varied, pitting closely comparable to that of *Dictyonella* is not known; such features as the net-like coscinidium of the richthofenacean *Sestropoma*, the surface pitting associated with spine development in the Productacea and the perforations on the brachial valve of the oldhaminidine *Coscinophora* are quite different structures and outside the scope of the present paper. The fine protegular pitting recognized on the chitinophosphatic acrotretides by Biernat and Williams (1970) and recently discussed by Bitter and Ludvigsen (1979) is not reconsidered here either, except where it is considered to have a bearing on the pitted ornament of the post-protegular shell.

THE PATTERNS OF PITTED ORNAMENTATION

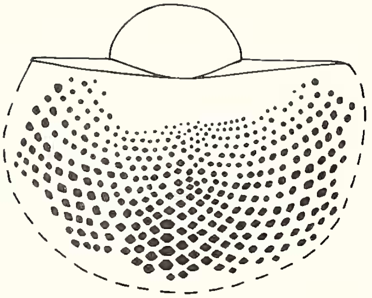
The patterns produced by the development of external pitting in some of these brachiopods appear to become very complicated. The sculptured surface of *D. capewellii* is 'very peculiar' according to Davidson (1869, p. 194), with the shape of the cells varying much both in size and shape and producing various patterns on different parts of the shell. Walcott (1912, p. 362) described the surface of the type species of *Dictyonina*, *Iphidella pannula* (White), as being 'as highly ornamented as that of any Cambrian brachiopod'; he went on to indicate that the ornament is 'formed of a very fine network of oblique raised lines, which divide it up into minute diamond-shaped, pore-like pits'. He further indicated the variation across the shell surface, and noted that posteriorly it has 'the appearance of oblique lines crossing at nearly right angles'. Attention is drawn to such oblique lines curving across the shell surface anteromedially from the lateral areas in many descriptions of *Dictyonella* (e.g. Bassett 1974, p. 81) and the feature is probably exhibited in its most extreme form in the obolid *Westonia* with its 'peculiar transverse semi-imbricating, 'ripple-embossed' lines that cross both the concentric and radiating striae' (Walcott 1901, p. 683). Walcott later (p. 691) drew attention to the puzzling, slightly backward curvature of the lines towards the margin.

In understanding these patterns of ornamentation, one of the basic problems has been that the studies have tended to look at the preserved pattern on the shell surface rather than to consider actual shell growth, and in particular the shell margin shown by that of the dead shell or by variably marked growth stages. Such examination of the growth of the shells reveals that all of these varied patterns are in fact produced by quite straightforward radial growth, with modifications arising by the inescapable geometrical results of packing radial rows of pits closer together, the commonly reduced and thus slower deposition of shell towards the postero-lateral margins, and the undulations of the mantle edge responsible for secreting the shell surface. The radial pits are very well illustrated by *Porambonites* (Pl. 70, fig. 4); the patterns of all other pitted ornaments are simply variations of this theme.

Taking the case of *Dictyonella* first, reference to the literature and to the specimens illustrated herein (e.g. Pl. 62, figs. 5, 9) shows that the basic form of the pit varies from rhombohedral to hexagonal. More attention has been paid to the eye-catching shell material forming the boundaries of the pits rather than to the pits themselves. In fact the rows of pits continue to radiate from the umbo, but to accommodate closer packing of the rows, the pits of adjacent rows become staggered in order to maintain an optimum separation between neighbouring pits (text-fig. 1A, B). When walls are developed between the pits (text-fig. 1C), these become more apparent than the pits and the radial nature of the latter is concealed as the pits of approaching adjacent rows become further separated radially (text-figs. 1D, E). The diagrams of text-fig. 1 give the stylized pattern resulting from purely anterior growth, which would only be approached in the middle sector of a large flat shell; the growing edge is in practice curved, so that the oblique lines which are well developed in patterns 1C and 1D would themselves be curved. Goryansky (1969, p. 104) described the picture of curved rows

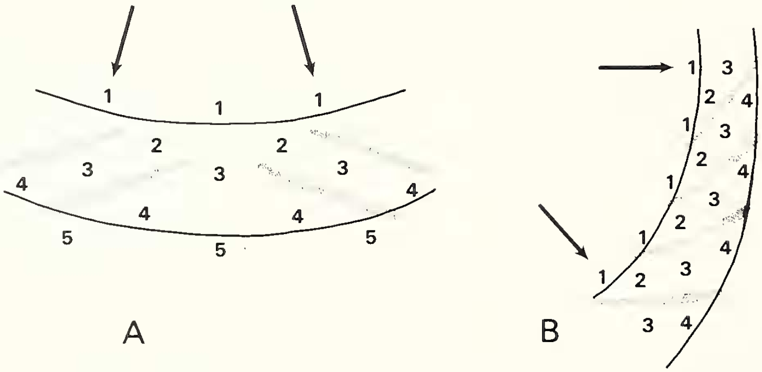


TEXT-FIG. 1. Diagrammatic representations of basic pit patterns, assuming growth on flat surfaces in the direction indicated by the arrows. A—radial rows; B—radial rows, more closely packed with offsetting of pits in adjacent rows; C, C′—pits as in B, but with well-developed walls to the pits as in *Dictyonella* in C, quincuncial pit pattern only in C′; D, D′—rows more closely packed producing rhombohedral walls; E, E′—closer packing of rows with radial distances between pits in each row increased and the development of parallel walls between pits of alternating rows to produce hexagonal walls; rows of pits still retain radial arrangement.



TEXT-FIG. 2. Diagram showing the arrangement of the pits of *Lacunites* in offset radiating rows. Based on the specimen figured by Goryansky (1969, pl. 20, fig. 10).

directed at an angle to the lateral edges of the shell and crossing over each other for *Lacunites*. Text-fig. 2 is based on his figured specimen (1969, pl. 20, fig. 10) and, despite the difficulty of interpreting the less well-defined parts of the original figure, the pits in the median sector are clearly seen to be arranged in offset radiating rows. Laterally, the radial rows are still present but less obvious, for the eye is caught by the curved arcs. It appears that each arc has its pits produced in a continuous sequence, but these arcs simply reflect the offsetting of successive radial rows of pits as the shell margin curves towards the posterior. The arcs of this shell essentially illustrate the mode of development of the 'irregular transverse lines, with zigzag pattern in middle of valves' of Rowell's diagnosis of *Westonia* (1965*a*, p. H268). Unlike the paterinid, this linguloid-shaped shell is further complicated by the hemiperipheral growth. The surface pits which define the lines in *Westonia* are very small, and in most specimens are barely discernible. They are, however, quite clearly seen to define the rib-like ornament in the well-preserved Pratt Ferry material of *Westonia superba* figured by Cooper (1956, pl. 11E). In these shells, the umbonal region has only growth lines for about the first mm. Thereafter, pits reflecting depressions in the mantle edge develop along the growing margin, but the pits of adjacent radial rows are staggered. This results in oblique raised ridges developing between the pits in the manner shown in text-fig. 3A. In actual shells some irregularities are produced by small variations in the position of appearance of the pits. While the ridges cut the valve margin at a low angle medianly, laterally the ridges cut the margin at a much higher angle and may curve posteriorly (text-fig. 3B). The precise orientation of the ridges laterally will depend on the extent to which the crowding of pits resulting from reduced secretion at the mantle edge were compensated for by wider spacing between the adjacent pits of radial rows.



TEXT-FIG. 3. Stylized representations to show the relationships between growth lines (solid), 'ribs' (stippled), and pits (numbered) at the anterior (A) and lateral (B) margins of *Westonia*. Numbers refer to successive arcs of pits in offset radiating rows.

The relationship of the inter-pit ridges to the shell margin in pitted shells is dependent on various growth factors, principally the direction and rate of growth of the shell margin in addition to the spacings between adjacent pits in the radial rows and between adjacent rows of pits, as is clear from text-fig. 1. The extreme development would occur with the rows of pits orientated perpendicularly to the shell margin, resulting in simple ribs as in *Linoporella*, or parallel to the margin to produce concentric ridges. The latter development may account for the origin of the strong concentric ridges of the dictyonellidine *Isogramma*.

After the classical works of Thompson (1917, 1942) much attention has been given to the geometrical patterns of growth in various living groups (e.g. Raup 1966; Gould and Katz 1975). Patterns of puncta in brachiopods, which are relevant in that at least some surface pittings are associated with endopuncta, have been discussed by Kemežys (1965) and Cowen (1966). Kemežys was impressed by the development of concentric rows of puncta parallel to the valve margin, with the puncta of successive rows being out of phase by half their separation to account for the quincuncial pattern. As already noted, in the case of the pitted ornament the radial growth factor, subject to modification by change in growth direction, would appear to be more fundamental than any concentric factor, for the lack of precise concentricity is apparent from the varying stages of completion of the pits along well-marked growth lines. Although Kemežys's model (1965, text-fig. 1B) depicting the recurving arcs of puncta on the flanks did not fit the pattern of puncta actually seen in *Magellania* (p. 317), the pattern produced for this model does tie in with the recurvature of the ribbing found in *Westonia*. Cowen (1966) found Kemežys's models to be unsatisfactory in some respects. Having reconstructed polygonal networks to highlight the distribution of puncta (p. 270), he concluded that there was no preferred concentric pattern and that the separation between puncta was both independent of direction and constant over a small area. The first point applies equally to surface pitting; the equal separation of pits applies to a certain extent, but commonly only in very small areas as the size of the pits can vary considerably; but directional independence does not apply to surface pitting, for a radial directional factor is important not only in those forms with exopuncta arranged along the crests of radial ribs but also in forms with pits arrayed in net-like polygons where the radial control is only seen if looked for carefully.

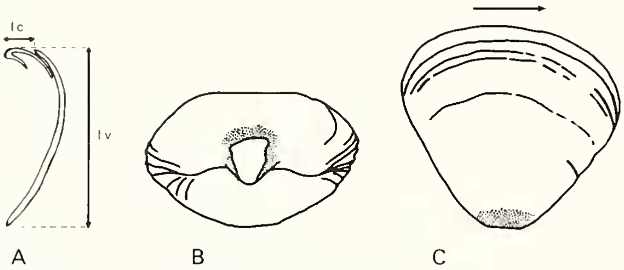
STRUCTURE OF *DICTYONELLA*

The triangular-shaped notch floored by the smooth plate in the umbonal region of the pedicle valve forms an area of shell surface on the fossil that is quite distinct from the net-like ornament of the remainder of the shell, and may conveniently be treated separately.

Umbonal region of the pedicle valve

Billings (1858) stated that the large valve was perforated on the umbo for the passage of the pedicle. Hall (1868, p. 274) quoted the description of *Eichwaldia* by Billings and gave a detailed description of the external and internal characters of his species *Eichwaldia reticulata*, illustrating the same type of denuded beak as in *E. subtrigonalis*. He observed that the ventral valve interior possessed a smooth, solid plate extending across the floor of the posterior part of the valve, separated from the outer shell anteriorly by a narrow slit at least across the width of the sulcus, and which extended posteriorly to form the smooth umbo. He remarked that while it was not usual for a pedicle to pass through a narrow slit in this position, the space evidently served for communication with the exterior.

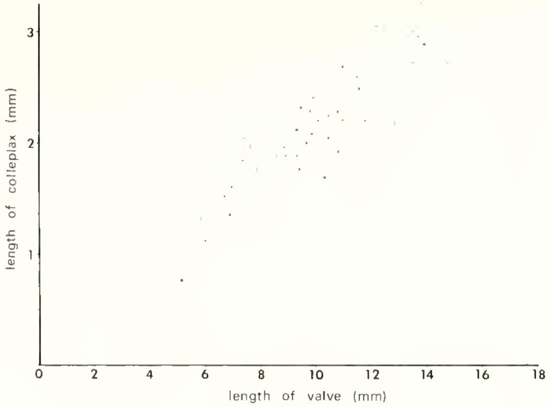
Davidson, in the absence of further information on the interiors of *Eichwaldia*, again quoted Billings. He went on to comment (1869, p. 193) that it is certain the type species 'was provided with a tolerably long pedicle, for Mr. Billings found a silicified specimen . . . in which this appendage had been wonderfully preserved'. Billings used acid techniques to extract his silicified faunas (1858, p. 191) and this particular specimen was illustrated in Davidson's figure A (1869, p. 192). Davidson, like Hall, commented that there was 'some uncertainty in my mind how the pedicle could have found space sufficient to protrude from under the concave plate' (op. cit.). This unusual specimen of *E. subtrigonalis* was again discussed by Hall and Clarke (1894, p. 310), this time illustrated from photographs and drawings provided by Mr. J. F. Whiteaves of the Geological Survey of Canada. Hall and Clarke comment 'notwithstanding this remarkable instance of the replacement of a soft organ by silica there seems . . . no reason to doubt that the umbonal aperture was solely for the passage of the pedicle'. Cooper (1952, p. 118) remarked the same 'specimen with a long projection extending from it which is said to be a pedicle'. Dr. T. Bolton (Geological Survey of Canada) and Dr. C. W. Harper kindly examined this specimen for me. Their conclusion is that the material purporting to be a silicified pedicle is simply adventitous silica adhering to the silicified shell.



TEXT-FIG. 4. Resorption of umbonal shell in *Dictyonella*; diagrams based on specimens of *D. reticulata* (Hall). A—longitudinal section of pedicle valve, showing measurements used in text-fig. 5; lc—exposed length of colleplax; lv—length of valve. B, C—posterior and ventral views of shell showing irregular and asymmetrical form of shell margin umbonally and interpretation of asymmetry in terms of orientation of the shell in the current (direction arrowed).

A detailed study of the umbonal region of *Dictyonella* was made by Young (1884). In his consideration of *D. capewellii* he showed that the margins of the reticulate shell adjacent to the triangular area were rough and rugged, with incomplete development of the polygonal cells. His interpretation of the frayed edges was that the animal was attached to marine objects by the substance of the shell, and had subsequently been broken away. Beecher and Clarke (1889, p. 32) pointed out that while the anterior margin is rough and irregular, the lateral edges appear invariably straight and diverge at an essentially constant angle. They indicated that the lateral sides represented the lines of attachment of the internal plate to the interior of the valve and fracture would take place along these lines if the shell were broken as suggested. As there is no aperture for protrusion of the pedicle along the cardinal margin, they suggested that the slit-like passage was either for the use of the pedicle or alternatively, as this space is so narrow, the valve was attached by shell substance with the internal shelf acting both to support the strain on the umbo and also to protect the animal should the shell be broken from its attachment.

I have examined *D. reticulata* Hall, a fairly abundant species in the Silurian Waldron Shale of Waldron, Indiana. These specimens confirm the irregular nature of the front of the triangular opening, but the lateral margins also show the incompletely developed polygons. Thus while the lateral margins are more or less straight posteriorly where the earlier formed polygons are smaller, some irregularity develops towards the front. Nevertheless, the irregular form of the front margin is usually much more apparent (Pl. 62, fig. 4 and Pl. 63, figs. 1, 2), and a sample (USNM 41023) has been assessed to check an impression that the right-hand side (as viewed forwards from the pedicle valve umbo) was longer than the left-hand side. Out of a sample of 60 shells, the anterior margin was essentially symmetrical in 37, clearly asymmetrical with the right-hand side extended in 15 and asymmetrical with the left-hand side extended in 8 cases. Thus where asymmetry is displayed, twice as many have the outer shell reduced on the right side of the plate as compared with the left, which



TEXT-FIG. 5. Graph showing the plot of the exposed length of the colleplax: length of pedicle valve for a sample of fifty-five specimens of *Dictyonella reticulata* (Hall) from the Waldron Shale, Waldron, Indiana.

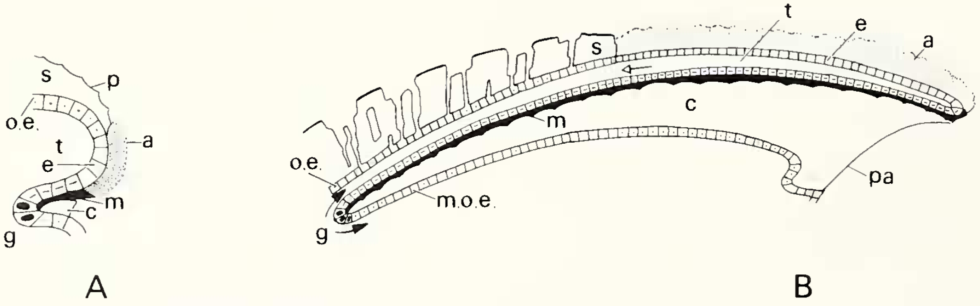
suggests a preferred orientation, at least in this random sample. This may be related to the orientation of the shell to the substrate (text-figs. 4B, C), the suggestion being that the outer shell may be reduced more readily where there is greatest pressure, i.e. in the downcurrent direction.

The sample was then assessed to ascertain the mid-line length of the exposed plate on the exterior relative to the length of the shell, both measurements being taken tangentially to the surface as indicated in text-fig. 4A. The plot of this distribution is shown in text-fig. 5, which suggests that the length of the triangular area increases as the shell grows. For this sample $n = 55$, and the correlation coefficient $(r) = 0{\cdot}8817$; on testing, $P < 0{\cdot}001$, indicating that the correlation between the two variates is significant. Such a correlation would not be expected if, as has been suggested by previous authors, the shell had simply been broken away from its position of attachment by, say, storm action. The implication of the correlation is that the earlier deposited surface shell must have been *resorbed* to allow for increased exposure of the underlying plate; the incomplete nature of the marginal polygons is also well explained by the process of resorption.

The exposed plate in the umbonal region of the pedicle valve is a type which is unique to the Dictyonellidina, and whilst the term 'notch' is appropriate for the approximately triangular area devoid of the normal shell of the exterior through resorption, it is not an appropriate term for the smooth area itself as was suggested for the genus *Isogramma* by Brand (1970, p. 70). Internally the plate produces a platform which does bear muscle scars, but the slit-like passage giving access to the exterior makes it a feature quite different from the muscle platforms present in a wide range of brachiopod genera, so that the term 'platform' does not convey the meaning specific to the dictyonellidine structure. Cooper and Grant (1974, p. 252) use the term 'pedicle plate' with reference to *Isogramma*, but as indicated already and discussed below, although the exterior of the plate served for attachment of the shell it is believed to be highly unlikely that the form of the organic material bore any resemblance to a pedicle in the accepted sense. Rather the plate is one by which the shell was glued to its substrate and the term *colleplax* (gr. kollesis-glueing; plax-plate or tablet) is here proposed for this structure.

The external surface of the colleplax of *Dictyonella* has been described as smooth (e.g. Bassett 1974, p. 81), and certainly it is when compared with the strong pitted ornament of the shell surface. The shell substance further lacks the obvious coarse punctation of the main shell; the microstructure is commented on below. Despite the relative smoothness, some fine details may be observed on the colleplax in various species. In *D. capewellii* well-preserved valves commonly show a median groove extending longitudinally along the surface. *D. reticulata* does not always appear to have this, but the whole surface is slightly roughened by the development of longitudinally arranged lines of very fine pustules. As regards size, the lengths of the latter are variable as the separation of pustules is commonly incomplete, but the width of the rows is of the order of 0·025 mm. A well-preserved colleplax on a specimen of *D. coralifera* (Hall) shows transverse ridges developed at the anterior of the exposed area (Pl. 63, fig. 3); these are interpreted as growth lines. Suggestions of similar growth lines may be seen on the colleplax of the Carboniferous *Isogramma salteri* Brand (Pl. 63, fig. 4), although these transverse ridges are much better displayed on a Permian specimen of *Isogramma* sp. figured by Cooper and Grant (1974, pl. 25, fig. 12); both these specimens show median and lateral lines on the colleplax. *Isogramma* differs from *Dictyonella* externally in its very strong concentric ornament and in achieving a much larger size; Cooper has figured an Upper Carboniferous valve over 18 cm in width (1952, pl. 21, fig. 1).

The envisaged method of function of the colleplax as an instrument of attachment to the substrate and the relationships with the soft tissue of the animal are illustrated in text-fig. 6. The attachment is by means of an adherent chitinous pad which in life covers the outer surface of the colleplax. While it seems likely that such a pad was already present in the larval stages to provide the means of attachment in the initial settling phase, it is uncertain how the organic material was related to the calcareous shell of the developing valve. Presumably it was located at the apex of the pedicle valve, but the process of resorption removed all traces of development of the apex as the shells grew, and specimens of the minute size which may provide evidence have still to be discovered. The simplest arrangement envisaged for young stages is shown in text-fig. 6A, with the chitinous pad being secreted by specialized epithelium comparable to the pediculate epithelium of the typical brachiopod. This passes rapidly into the surrounding standard outer epithelium for *Dictyonella*, the cells of which would be produced by the generative zones at the mantle edge where one could expect successive secretion of mucopolysaccharide, periostracum, and primary and secondary calcite layers as in extant calcareous brachiopods (Williams 1968*b*).



TEXT-FIG. 6. Stylized longitudinal sections of the umbonal regions in (A) young and (B) adult stages of *Dictyonella* to show the envisaged relationships between epithelium, colleplax, and outer shell. a—chitinous attachment pad; c—colleplax; e—epithelium secreting attachment pad; g—generative zone; m—mucopolysaccharide; m.o.e.—modified outer epithelium; o.e.—outer epithelium; p—periostracum; pa—palintrope; s—shell of pedicle valve; t—connective tissue. Empty arrow—direction in which resorption of shell takes place; solid arrows—direction of movement of cells away from generative zone.

EXPLANATION OF PLATE 62

Figs. 1, 2, 4, 10. *Dictyonella reticulata* (Hall). Waldron Shale (Silurian), Waldron, Indiana. 1, 2, 4, lateral, ventral, and posterior views of large shell, USNM 303732, ×3; 10, dorsal view of conjoined valves, USNM 303733, ×6.

Figs. 3, 6, 7, 8. *Dictyonella gibbosa* (Hall). Decatur Formation (Silurian), Linden, Tennessee. 3, 6, 7, ventral and posterior views of exterior, antero-dorsal view of interior of pedicle valve, USNM 303728, ×4, ×5, ×5; 8, interior of brachial valve, USNM 303729, ×4.

Figs. 5, 9, 11. *Dictyonella capewellii* (Davidson). Wenlock Shales (Silurian), Buildwas, Shropshire. 5, dorsal view of conjoined valves, BB 93771, ×6; 9, 11, postero-dorsal view of conjoined valves, and detail of surface of brachial valve, BB 93225, ×6, ×15.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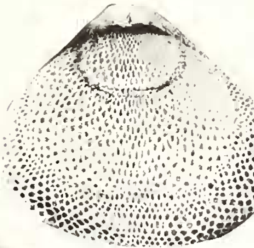
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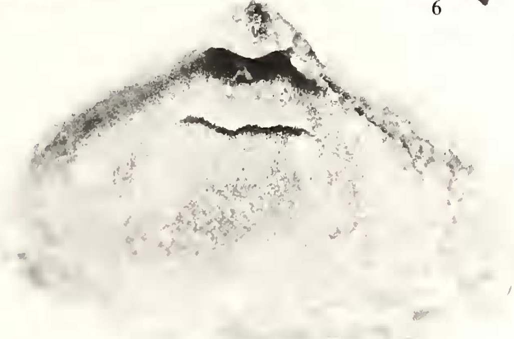
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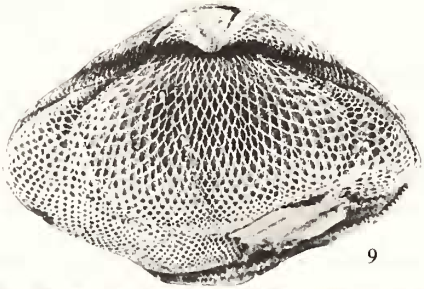
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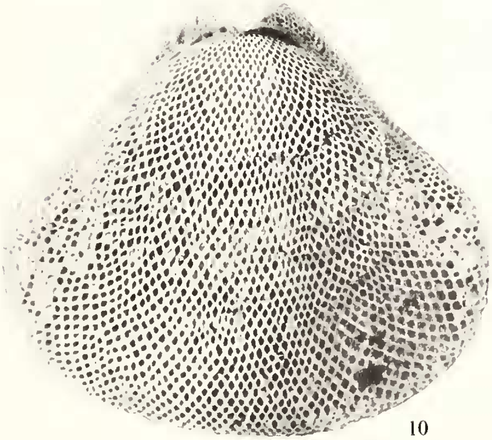
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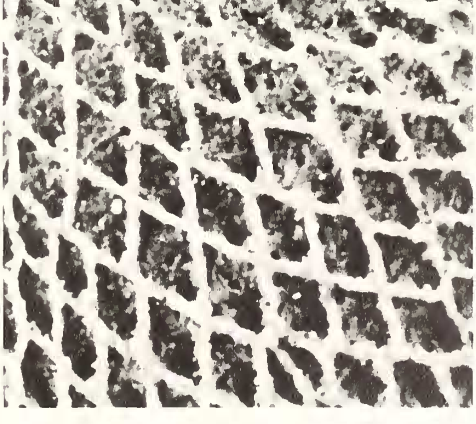
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WRIGHT, *Dictyonella*

To account for the resorption of the shell in the postero-median sector of the pedicle valve and the corresponding increase in surface area of the attachment pad, the outer epithelial cells must undergo physiological change in order to replace their secretory function by that of resorption and concomitantly to exude organic material for the chitinous pad. The physiological process would successively affect each arc of outer epithelial cells anterior to those already secreting pad material. The presence of a cavernous shell, with pits and puncta lined with caeca, no doubt facilitated the chemical resorption of the shell; and while the physiological changes in the cells would be related to chemical substances derived via the connective tissue, it is to be expected that proteins and other chemicals for pad production, and possibly even for shell resorption, would have been stored within the caeca as envisaged by Williams (1968*a*, p. 30) for the articulate brachiopods and by Williams and Wright (1970, p. 32) for the non-articulate *Crania*. In this context it is interesting to note that the shell of *Isogramma*, although lacking any surface expression of pits or puncta, is described by Cooper as having a 'spongy interior' (1952, p. 117) as a result of the closely crowded nature of the puncta on the inner shell surface. The increase in size of the attachment pad in adult shells, reflecting the anterior advance of the metamorphosis of the outer epithelial cells, is indicated in text-fig. 6B.

The colleplax, which internally extends much further anteriorly than is apparent from the exterior, must start to develop before resorption affects the outer shell at the umbo. Its development antero-dorsal of the initial attachment area is controlled by a generative zone of epithelium situated at the anterior margin of the colleplax (text-fig. 6A, B). Here it is envisaged that two sets of cells are secreted behind the generative zone, which thus migrates anteriorly. The cells are pushed out on to either side of the colleplax. Those on the outer (ventral) side would secrete mucopolysaccharide and serve to attach the whole organic pad to the calcareous material of the colleplax, roughened by growth lines produced by the pulsatory calcareous deposition along its anterior growing edge. The colleplax itself would be secreted by the cells developing from the inner (dorsal) side of the generative zone. Laterally this colleplacial epithelium must pass into the standard outer epithelium of the shell at the margins of the colleplax. The modified outer epithelial cells secreting the colleplax continued to secrete calcareous material across its entire surface through the life of the animal so the colleplax is thickest posteriorly. The posterior surface, which although curved right over the brachial valve umbo (Pl. 62, fig. 10), is exposed to the exterior and forms a palintrope. To enable growth of this structure (Pl. 62, fig. 7), new cells would also need to be generated at its anterior growing edge.

This model accounts for (1) the differentiated inner surface of the colleplax and its formation of calcite structurally distinct from the main shell; (2) the growth ridges on the exterior of the colleplax; (3) the retreat of the shell anteriorly by resorption and the abraded nature of the marginal polygons; (4) the mode of attachment to the substrate and the function of the narrow passageway. The height of this passageway in the large (12 mm long) figured silicified pedicle valve of *D. gibbosa* (Pl. 62, fig. 6) is 0·15 mm, although the actual height may have been somewhat less as a possible etching effect may have increased the height of the opening. To compare this distance with the relatively small pedicle foramen in some strophomenidines, a sample of ten specimens of *Leptaena richmondensis* Foerste from the Upper Ordovician Waynesville Formation of Indiana whose disc size is about 14 mm was measured and showed a mean length for the foramen of 0·8 mm. Similar measurements for ten specimens of *L. oklahomensis* Amsden from the Silurian Henryhouse Formation of Oklahoma whose disc size ranged from 5 to 7 mm had modal lengths of 0·2 to 0·3 mm, although in this species the foramen becomes sealed to a greater or lesser extent by shell tissue. Despite the relative narrowness of the passage in *Dictyonella* the organic tissue emerges across a widening surface which would enable the development of an adequate pad for adherence to the substrate.

Apart from the lack of pitted ornament and its generally smooth appearance, the details of the shell substance of the colleplax are not well documented. The difficulty of ascertaining whether or not the colleplax was punctate was noted by Young (1884, p. 215), and although he established that the 'inner shell layer' was finely punctate it seems unlikely from his subsequent discussion that this was confirmed for the colleplax. The present study indicates that the colleplax does possess fine puncta, but they do appear to be indifferently developed or preserved. The outer surface, when well preserved, may show small depressions in the calcite of the colleplax which could mark the position of puncta.

The only good interiors available for examination were in the Decatur material, which is silicified; however, cellulose peels of longitudinal sections through the colleplax of *D. reticulata* do show sporadic fine puncta (Pl. 66, fig. 7), which have been confirmed in S.E.M. studies of the same species despite the recrystallized nature of the shells.

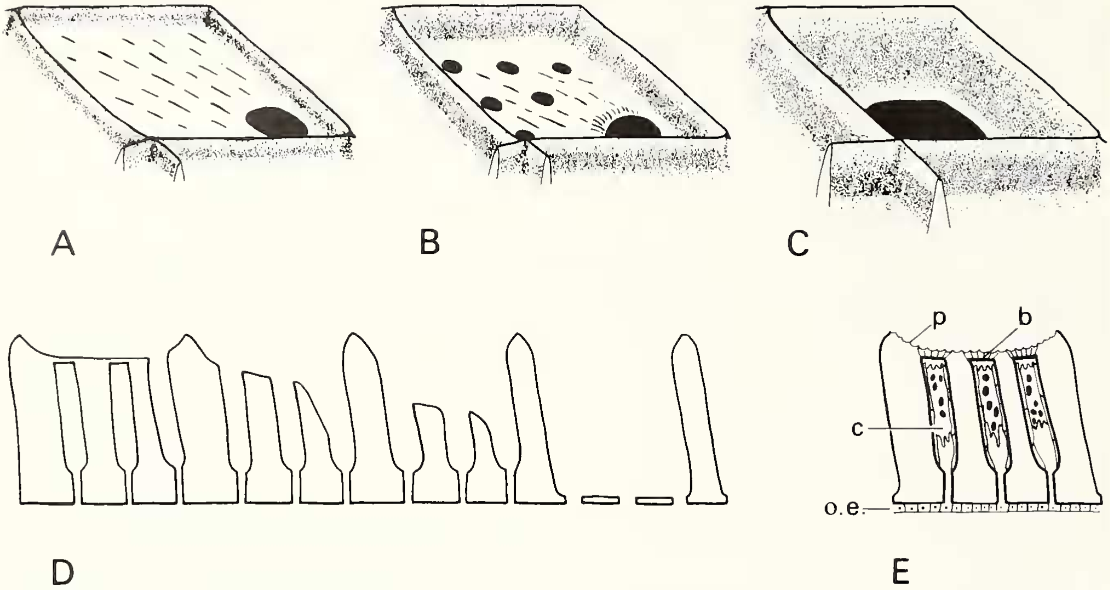
The punctation of the colleplax is more readily ascertained in the Isogrammidae and its undoubted presence was clearly indicated by Cooper for the Permian *Megapleuronia* (1952, p. 118). In *Isogramma* some interesting variation is shown which may be a reflection of the situation in the earlier stocks. The type specimen of *I. salteri* Brand (IGS Zo1525) from the Brigantian Hotwells Limestone of Somerset is a well-preserved disarticulated pedicle valve. On the interior, the merging of the shell with the lateral margins of the colleplax is clearly marked by an abrupt disappearance of the coarse punctation of the main shell. However, close to the apex of the colleplax, punctate shell is seen to have developed across the inner surface, while in an associated specimen (IGS Zo1517) whose interior is filled with limestone matrix, punctation is clearly visible over that part of the colleplax which is exposed on the surface.

The surface of the main shell

The surfaces of the mid-Silurian *D. capewellii* and *D. reticulata* represent an advanced stage in the development of the reticulation of the *Dictyonella* shell, with the rhomboidal or hexagonal pits large and separated by high, narrow ridges of shell which produce the characteristic net-like effect. In the *Dictyonella* from the late Ordovician of the eastern mid-Continent figured by Amsden (1974, pl. 25, figs. 1, 2) the net-like appearance of the surface is less obtrusive and the pits themselves are smaller. Attention was drawn to this latter point by Amsden (p. 78), who noted that individual specimens of forms such as *D. reticulata* show considerable variation in pitting. Examination of his figured specimen USNM 169252 from the Noix Limestone of Missouri shows that the pits attain a length of 0·12 mm, but are modally about 0·1 mm and somewhat smaller posteriorly. On the specimens of *D. reticulata* figured herein (e.g. Pl. 62, fig. 10) the modal length is of the order of 0·25–0·3 mm, although in the large specimen (Pl. 62, fig. 2) many smaller pits of about 0·1 mm do occur. The important feature of the Noix shell would appear to be that the pits do not attain the large size of the later forms. Smaller pitting is characteristic of the slightly older form described herein as *Dictyonella planicola* sp. nov. from the Ashgill Boda Limestone of Dalarna, Sweden (Pl. 63, fig. 9). An interesting feature of this shell is that the net-like appearance only develops after about 5 mm of anterior growth, where the pits are about 0·15 mm long; towards the front of the shell the pits attain a length of 0·2 mm. Over the posterior portion the shell is simply pitted, lacking the network resulting from differential shell deposition between the pits. Coupled with the very small size of the pits near the umbo (0·04 mm long), it suggests that *D. planicola* represents a morphological stage in the development of the strongly reticulate pattern from the presumed ancestral smooth *Eichwaldia* stock.

The Ludlow specimens of *D. gibbosa* from the Decatur Formation are silicified and the preservation generally poor. In a relatively well-preserved small shell (Pl. 63, fig. 5) the pits are rhomboidal, up to about 0·28 mm long and 0·2 mm wide, with the pit floor dipping sharply anteriorly and a well-developed punctum about 0·05 mm wide plunging into the shell at the front angle of the rhomb with several much less obtrusive and finer pits posteriorly (Pl. 63, fig. 6). It is not possible to say in all cases whether the finer puncta are developed on the floor posterior to the main punctum. On the valve interior, only a few scattered puncta with a diameter of about 0·02 mm are preserved near the margin of the shell. A large specimen (Pl. 62, fig. 3) appears to have much smaller but variable pits on the exterior with the lengths of two adjacent pits near the front being 0·16, 0·24 mm (Pl. 63, fig. 11). Again the pits plunge deeply into the shell and have a surface density essentially the same as that of the puncta opening on to the shell interior (Pl. 63, fig. 12); these also have a diameter of about 0·02 mm, indicating an inward constriction.

In *D. capewellii* and *D. reticulata* not only does the outline of the pits vary as already indicated but the contained structure also appears to vary markedly. The external surface contained by the walls of the polygon varies from being only moderately depressed below the boundary walls, when it may contain anything from a single punctum up to nine puncta (Pl. 62, fig. 11; Pl. 65, figs. 5, 6), to a



TEXT-FIG. 7. A, B, C—sketches of surface pits of *Dictyonella* showing variation of boundary walls, floor, and contained puncta (solid black), interpreted as stages in breakdown of internal walls. D—sequence of envisaged breakdown in longitudinal section. E—longitudinal section of pit showing inferred distribution of soft tissue. b—caecal brush; c—core cells of caeca; o.e.—outer epithelium; p—periostracum.

situation where the walls contain a deep pit of almost their own dimension, with the puncta only present in a thin shell layer deep in the pit which separates the pit from the shell interior (text-fig. 7). These varied forms appear to be best interpreted as stages in the breakdown of fine calcite sheaths to the puncta; where preservation of the shell is especially poor, the pits as such pass straight through the valve without preservation of the much narrower internal opening of the puncta. Apart from these envisaged changes affecting the valve floor the walls of the pits may also be abraded (Pl. 63, fig. 7). In this case the calcite walls of each punctum produce a variably developed halo of micropits around the reduced main pit. Further abrasion may affect the puncta in the centre of the pit so that the whole area shows a honeycomb structure of even-sized pits, which represents the 'polygonal cell layer' of Young

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EXPLANATION OF PLATE 63

Figs. 1, 2, 8. *Dictyonella reticulata* (Hall). Waldron Shales (Silurian), Waldron, Indiana. 1, umbonal region of pedicle valve showing colleplax, USNM 303733, × 6; 2, detail of colleplax, USNM 303734, × 15; 8, surface of brachial valve showing relationship of growth lines to pitting, USNM 303734, × 15.

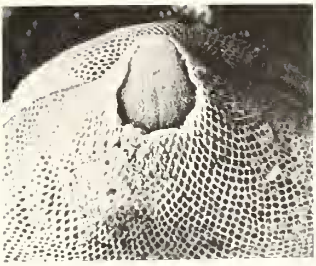
Fig. 3. *Dictyonella coralifera* (Hall). Rochester Shale (Silurian), Lewistone, New York. Pedicle valve umbo showing detail of colleplax, USNM 303727, × 15.

Fig. 4. *Isogramma salteri* Brand. Hotwells Limestone (Carboniferous), Compton Martin, Somerset. Colleplax in pedicle valve, IGS Zo1525, × 6.

Figs. 5, 6, 11, 12. *Dictyonella gibbosa* (Hall). Decatur Formation (Silurian), Linden, Tennessee. 5, 6, exterior of small pedicle valve and detail of surface, USNM 303730, × 5, × 15; 11, exterior of pedicle valve, USNM 303728, × 10; 12, interior of brachial valve of comparable size, USNM 303729, × 10.

Figs. 7, 10. *Dictyonella capewellii* (Davidson). Wenlock Shales (Silurian), Walsall, Staffordshire. Exterior and interior surfaces of a brachial valve, BB 93772, × 15.

Fig. 9. *Dictyonella planicola* sp. nov. Boda Limestone, (Ordovician) Solberga, Dalarna. Detail of brachial valve exterior, Riksmuseum, Stockholm, Br 108470, × 15.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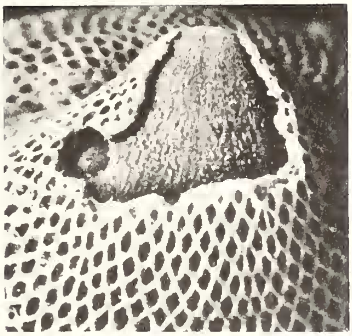
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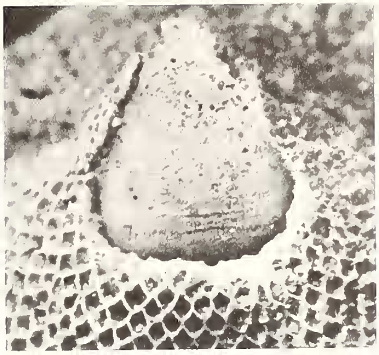
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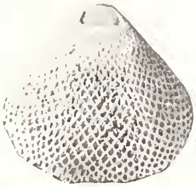
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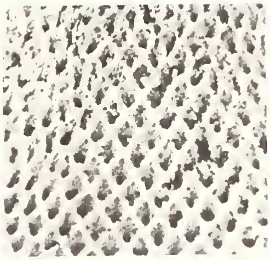
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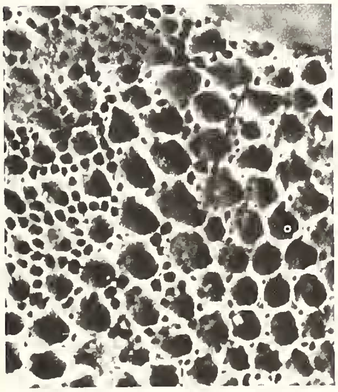
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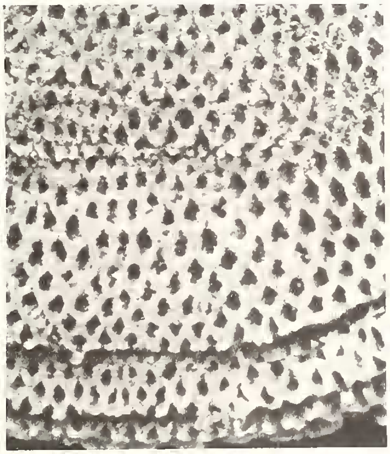
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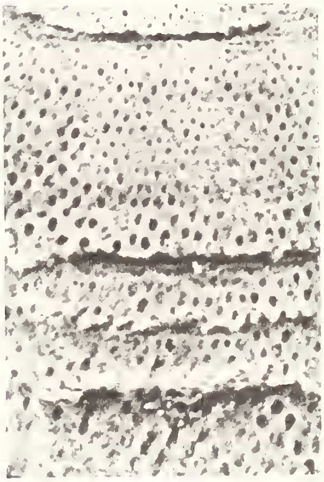
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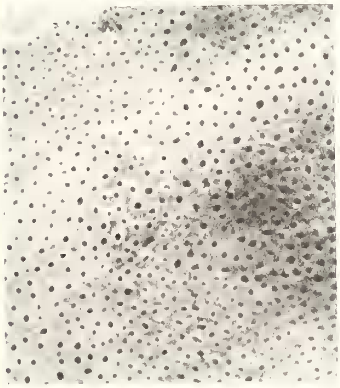
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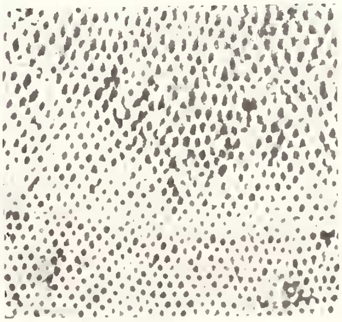
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WRIGHT, *Dictyonella*, *Isogramma*

(1884, p. 217). Each of these micropits marks a punctum which opens on the valve interior, the comparable spacings and densities being shown in Plate 63, figs. 7, 10. The polygonal network would appear to be related to the possession by individual puncta of stouter calcareous sheaths than those with sheaths which subsequently collapsed to form a single large pit in the fossil.

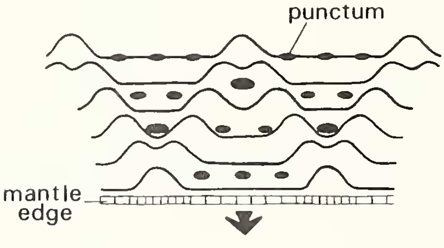
On this interpretation there seems little reason to regard the puncta within the pits of *Dictyonella* as being basically very different from the typical puncta of articulate brachiopods. Presumably they also housed caecal extensions of the mantle as indicated in text-fig. 7E. The apparent absence of puncta from the floor of some pits, or the recognition that some puncta do not reach the outer surface in sections of shell, is a normal feature of endopuncta. If preservation were adequate, one would expect to find evidence of the penetration of the shell immediately overlying the punctum by the cytoplasmic threads of the caecal brush (Owen and Williams 1969), but although promising looking specimens were examined in the scanning electron microscope, no such very finely perforated canopy of primary shell was observed.

The problem as to whether the pits contained soft tissue or whether this was restricted to the narrow canal between the pit and the interior of the shell was commented upon by Williams (1968*a*, p. 49, text-fig. 26). The present study would indicate that soft tissue lined all the cavities within the well-preserved shell as indicated in text-fig. 7E. Longitudinal sections of a specimen of *D. reticulata* which show the relationship between the pit floor, the 'polygonal cell layer', and the narrow proximal ends of the puncta are illustrated in Plate 66, figs. 1-4. Whether the periostracum was adherent to the relatively shallow surface of the pit below the boundary network of ridges or was stretched across from the crests of the boundary ridges is debateable. A *Dictyonella* valve with an epizoan overgrowth across the mid-valve surface was sectioned, and the relationship between the reticulated valve surface and the epizoan examined under S.E.M. A montage indicated that the calcareous floor of a basal zooecial (?) chamber extended straight across from the ridge on one side of the pit to the other, suggesting that either periostracum was present in this position and formed a floor across which the epizoan grew or the epizoan grew across sediment filling the pit after death and decay of the soft tissue of the animal. Neither possibility resolves the problem. What can be said is that the epizoan did not grow down into and across the pit; but whether the epizoan growth would have followed such detailed topographic variation is unknown.

Study of the various well-defined growth stages shows the polygons of the network to be in various states of completion, usually with lateral gradation, at any particular growth stage (e.g. Pl. 63, fig. 8). The margins of the pits are produced by zones of increased secretion at the mantle edge which oscilliate laterally with growth (text-fig. 8). In between these zones the floors of the pits are much thinner. In some cases it appears that the shell had a serrated margin but as growth lines may be traced straight across the valve surfaces, the shell clearly grows with a smooth arcuate margin so that the serration must simply reflect the fragile nature of the thin shell of the floor of the pit when exposed at a well-marked growth stage or at the shell edge.

Shell structure

Young, in his study of the shell structure of *Dictyonella*, described the shell between the perforations of the 'inner layer' as being dense and having a minutely granular structure 'which may be partly due to slight change through the action of mineralization' (1884, pp. 215-216). The last point was reiterated later (p. 218) when he emphasized the need to examine specimens 'in which the shell



TEXT-FIG. 8. Stylized sketch of the shell margin in *Dictyonella* to show the development of pit walls by the lateral migration of increased zones of shell secretion at the mantle edge.

structure has suffered little change through crystallization', and this problem of recrystallization to a greater or lesser degree has proved to be a problem with the current S.E.M. studies of the shell structure. Williams (1968*a*, p. 48) indicated that the ultrastructure of the shell was quite distinct from even recrystallized rock matrix, and accordingly attributed the observed differences to the state of the fabric during life. In view of the lack of lineation in the shell related to either the internal surface or the puncta, he concluded that the ultrastructure was closer to that of the primary layer of the standard articulate shell. The inner surface of a sectioned pedicle valve of *D. capewellii* penetrated by a micrite filled punctum is illustrated in Plate 64, fig. 1, in which the irregular fabric of the shell shows only a very rough alignment to the margin of the punctum, while adjacent to a nearby punctum the fabric is overprinted by calcite cleavage parallel to that of the micrite filling the punctum (Pl. 64, fig. 2).

However, although the irregular fabric as described by Williams is usual, one transversely sectioned specimen of *D. capewellii* shows several grains very closely comparable in form to cross-sections of the fibres of the secondary shell in Recent rhynchonellides and terebratulides as illustrated by Williams (1966, 1968*a*). This shape was only well observed within 10 μm or so of the inner surface of each valve, and then only at one end of the shell as preservation deteriorates laterally along the valve. The sections (Pl. 65, figs. 1–3) show an outer surface of two lateral areas joined by a median saddle, all concave outwardly, and a roundedly convex inner surface as in the standard fibre. Passing outwardly these distinctive sections become less clearly marked. One of the features noted by Williams, and present in the shells examined here, are well-developed channels and pittings within the shell mosaic which were ascribed by Williams to microvillous trails (1968*a*, p. 48). These impart a 'spongy' texture to the shell on the microscale and, in addition to the highly punctate and spongy nature of the shell on the macroscale commented on above, may well account for the ready alteration of the shell of this genus.

The radially orientated fibres on the variably weathered floors of the surface pits are shown in Plate 64, figs. 4, 5, again with the fine pittings of the shell fabric well displayed. At the edge of the pits the shell may become steeply inclined (Pl. 64, fig. 3) while in other specimens the inter-pit ridges appear to be composed of flat-lying laminae (Pl. 64, fig. 5).

Evidence for the primary layer is scant, but it appears to have been preserved occasionally in the sediment-filled pits of the external ornament. The thickness of the primary layer shown in Plate 65, fig. 4 is about 3 μm.

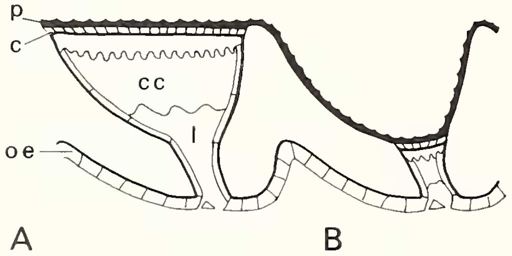
PITTED SURFACES OF PUNCTATE ARTICULATE BRACHIOPODS

Various types of pitting occur on the surface of the shell of punctate articulate brachiopods, but the patterns which most closely resemble those of *Dictyonella* are those producing a reticulate shell surface, with the pits associated with puncta which pass through the shell substance to open on the interior of the valve. The genera falling into this category include the punctate orthidines *Saukrodictya*, *Oanduporella*, *Fascifera*, *Pionodema*, and some species of *Dalmanella*.

Saukrodictya. The ornament resembles that of *Dictyonella* in being composed of polygonal pits but differs in that the pitting is associated with a clear radial ornament of costae and costellae (Pl. 67, fig. 8). Although the original material of the type species is silicified and does not show any sign of punctation (Wright 1964, p. 219), Temple (1970, p. 33) was able to demonstrate from mould material that the relatively large surface pit opens directly from a punctum which passes through to the inner surface of the shell. This is well shown by the external mould figured herein of a specimen from Maine collected by Dr. R. B. Neuman (Pl. 68, fig. 5). The roundedly polygonal pits attain a diameter on this specimen of about 0·15 mm, but it is noteworthy that the size of the pits grades down to 0·02 mm. The pattern of pit development reflects a close packing system confined by the ribs, with a single row rapidly becoming a staggered double row with additional pits developing to occupy the intercostal space available. In general, but not entirely, pits tend to increase in size as the shell grows. In the specimens from Wales (Pl. 67, figs. 2, 8) described by Hiller (1980), the diameter of the preserved pits ranges from 0·05 up to 0·28 mm; a very delicate specimen preserved as an external mould in mud etched from the Ashgill Chair of Kildare Limestone shows pits of up to 0·15 mm diameter.

These moulds reveal that the relatively broad pits are rounded on their lower surface, with an abrupt change in diameter as the narrowly cylindrical internal part of the punctum is reached. In the case of the smaller pits, the moulds indicate that these result from the cylindrical portion passing through the shell with little increase in diameter as noted by Temple (1970, p. 33). In all cases where preservation of the proximal cylindrical stalk infilling is clear, it is present simply as a single rod of matrix; this again is in contrast to *Dictyonella*, where the external pit commonly defines an area containing several puncta.

As there is undoubted evidence of a passage from the external pits to the inside of the shell, it is reasonable to interpret this as indicating the presence of caecal invaginations of the mantle. At the internal end, the diameter of the punctum, of the order of 0·02 mm, is within the expected size range indicated for punctate articulate stocks by Thomson (1927, p. 104) and Owen and Williams (1969, p. 189); but the diameter reached by the pits at their external margin is well in excess of any 'normal' punctation. From an interpretative viewpoint the problem is whether the pit in its entirety was filled by a caecal invagination with an unusually large caecal head which would be covered by a thin canopy of calcite separating it from the periostracum extending across the surface (text-fig. 9A) or whether the pit was lined with periostracum and the caecal invagination restricted to the proximal tubular portion. In the latter case the net-like polyzoan appearance of the surface would be very evident, and it could be argued that this would be advantageous in inhibiting the settling of epizoans. Alternatively, if the pits acted as repositories for various chemicals, including toxic elements, which could be exuded on to a more even external surface through the periostracal cover, this might be a much more satisfactory method of discouraging settling or boring organisms. A second point, supporting the filling of the pits by organic tissue, concerns the morphology. The deep pits are not symmetrical in that the internal punctum is situated at the anterior end. Further the pits commonly, but not invariably, open outwards in a posterior direction, with the proximal narrow punctum similarly orientated in most of the material here examined. This arrangement is very similar to that observed in *Sarganostega*; in that form additional morphological detail supports the view that it contained an unusually large caecum, and accordingly I would view the interpretation depicted in text-fig. 9A as more likely to be correct.

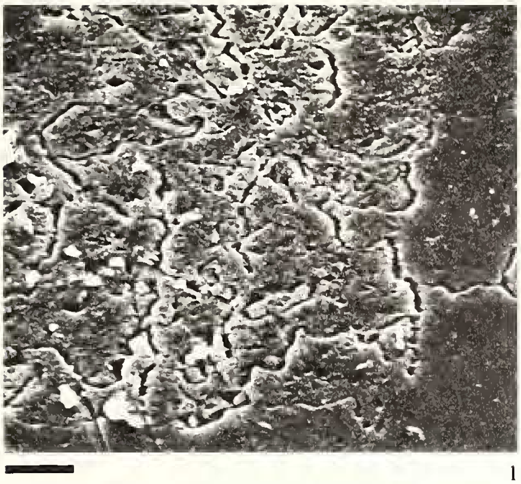


TEXT-FIG. 9. A, B—two alternative interpretations of the distributions of periostracum, caecum, and outer epithelium within the pits and puncta of the *Saukrodictya* shell. Longitudinal section, anterior to the right; c—calcite canopy; cc—core cells; l—lumen; oe—outer epithelium; p—periostracum.

EXPLANATION OF PLATE 64

Figs. 1, 2, 3, 6. *Dictyonella capewellii* (Davidson). Wenlock Shales (Silurian), Buildwas. 1, 2, polished and etched longitudinal sections of pedicle valve, BB 93226, scale bars 5 μm. 1, inner surface of shell showing irregular shell mosaic, junction with micrite filling shell interior at bottom with punctum along right margin; 2, punctum entering internal surface of shell from bottom left. Calcite cleavage of infilling overprinting shell mosaic; 3, detail of Plate 4, fig. 6 showing nature of shell at pit margin, punctum present at base of rim, BB 93227, scale bar 10 μm; 6, external surface near front margin of brachial valve showing pit with three puncta and a large anterior punctum, BB 93228, scale bar 50 μm.

Figs. 4, 5. *Dictyonella reticulata* (Hall). Waldron Shale (Silurian), Waldron, Indiana. USNM 303740. 4, detail of pit floor showing fibres with pitting and some calcite recrystallization, scale bar 5 μm; 5, surface features showing disposition of calcite in walls of pits, puncta and variably preserved shell, scale bar 50 μm.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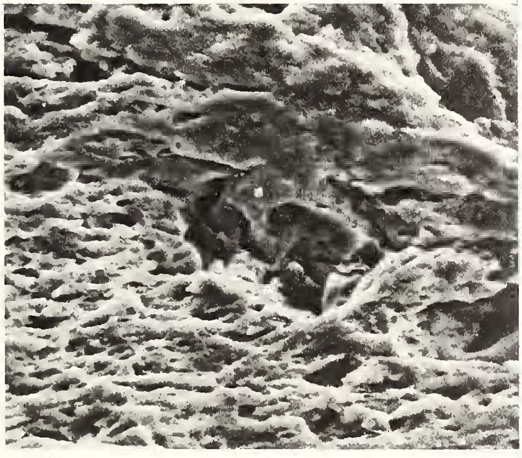
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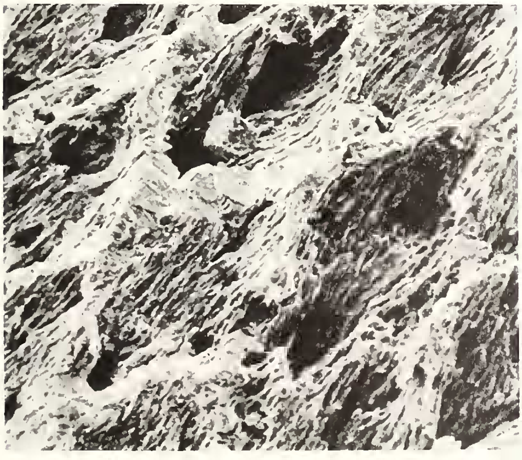
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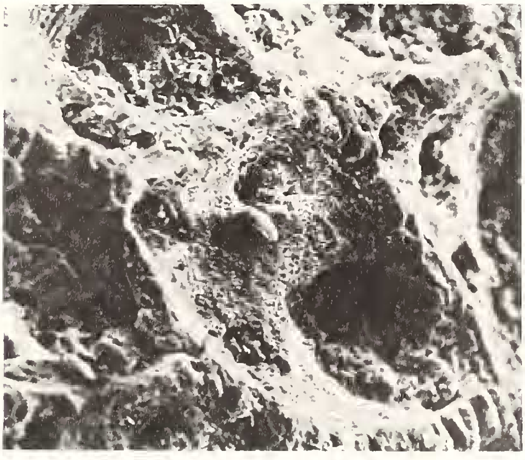
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WRIGHT, *Dictyonella*

Oanduporella and *Fascifera*. The draboviinid *Oanduporella* is morphologically close to the genus *Fascifera*, but according to Hints (1975, pp. 19, 105) it may be distinguished by stronger ribbing, longer dorsal adductor scars, and a net-like microsculpture between the ribs. From Hints's illustrations (1975, pl. 1, figs. 11, 12) the pits open perpendicularly to the shell surface and represent the external manifestation of the caeca which occupy the puncta of the inner shell surface. The net-like microsculpture is produced by extra calcite secretion at the mantle edge in those cells surrounding the puncta. The development of the pattern is again a reflection of the amount of space available between the ribs which control the degree of development of the meshwork. As costellae branch off from the costae, a single row of pits develops in the narrow space; with further growth, the widening of the intercostal spaces permits the successive development of staggered rows, double rows, quincuncial pitting, and so on. Unlike *Saukrodictya* the external pits appear to be of closely comparable size and about 0·1 mm in diameter in Hints's figures (1975, pl. 1, fig. 12; pl. 2, fig. 5).

A similar type of network is developed in *Fascifera stonensis* (Safford), which is referred to by Cooper (1956, p. 1001) as having 'spaces between costae coarsely punctate'. This is shown in Plate 69, figs. 2, 4, but although the pitting is undoubtedly developed, the siliceous preservation of this material does not show the more precise detail seen in the cited *Oanduporella* figures. The pits appear to be about 0·05 mm in diameter, but while staggered rows are visible in places, elsewhere the arrangement appears to be that of concentric arcs of pits separated by concentric ridges of shell. Another feature of the surface of *Fascifera*, seen also in the closely related *Pionodema* but not on *Oanduporella*, is the presence of sporadically developed exopuncta of the form commonly referred to as hollow ribs (Williams and Rowell 1965, p. H68, fig. 72). These structures are here considered below in connection with *Rhipidomella*.

Dalmanella. A pitted ornament occurs in some species of *Dalmanella* such as the middle Ordovician *D. sculpta* Cooper (Pl. 68, figs. 3, 7) and *D. costellata* Cooper, and in a new form provisionally assigned to *Dalmanella* cf. *sculpta* by Williams and Wright (1981) from strata of Ashgill age to the north of Llandovery at Garth (Pl. 69, fig. 1). The pitting effect in these forms is seen in the interspaces between the ribs and is produced by concentric growth line undulations of the shell separating concentric arcs of standard puncta. In *D. sculpta*, the concentric ridges forming the ornament are set about 0·08 mm apart with apertures of the puncta about 0·02 mm in diameter; in the Garth shells the ridges are similarly spaced but shorter, so that the apertures are proportionately larger, between 0·025 and 0·05 mm. The arcs of puncta are developed before each new growth undulation, with additional rows of puncta appearing normally without showing the offset pattern noted above. However, at least in the type collection of *D. sculpta*, a zig-zag row of very much less dense and slightly larger (*c.* 0·03 mm) puncta develop along the ribs themselves (Pl. 69, fig. 7). These are here interpreted as exopuncta; at the front of the shell they are raised from the ribs on cones of calcite to give a beaded appearance to this part of the rib as noted by Cooper (1956, p. 951), with the apertures somewhat forwardly directed (Pl. 68, figs. 4, 8). These punctations give a similar if less pronounced appearance to the ribs as those found along the crests of the ribs in many species of *Paurorthis*; the oblique anterior orientation outwards from the shell surface of such puncta was commented on for a sample of *Paurorthis* sp. of early Ordovician age by Neuman (1977, p. 23). But as regards the pitted

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EXPLANATION OF PLATE 65

Figs. 1–6. *Dictyonella capewellii* (Davidson). Wenlock Shales (Silurian), Shropshire. 1–4, polished and etched transverse sections, BB 93229. 1, inner edge of brachial valve. Junction with micrite filling shell interior near bottom, portion of infilled punctum at top right, scale bar 5 μm; 2, inner edge of pedicle valve. Junction with micrite filling shell interior near bottom, scale bar 5 μm; 3, detail of fibres of Figure 2, scale bar 2 μm; 4, outer edge of pedicle valve with sediment in lower right succeeded by primary layer with secondary layer in upper part of figure, scale bar 2 μm; 5, 6, part of external surface, with detail, showing network of pits with contained puncta, BB 93227, scale bars 100 μm.


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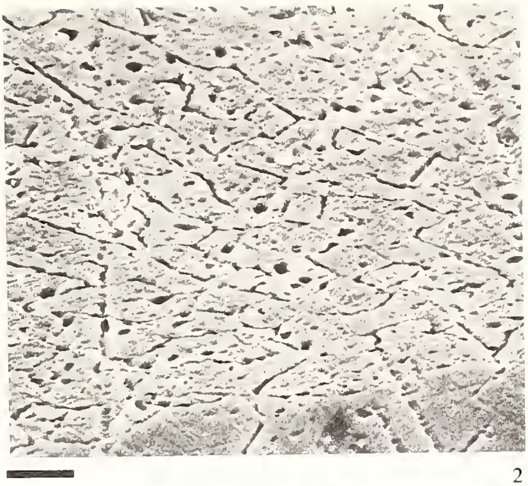
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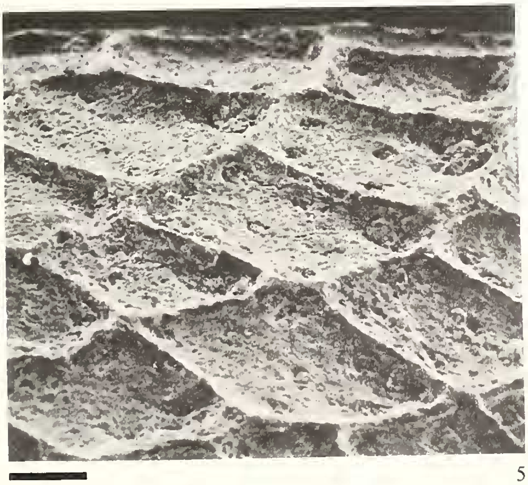
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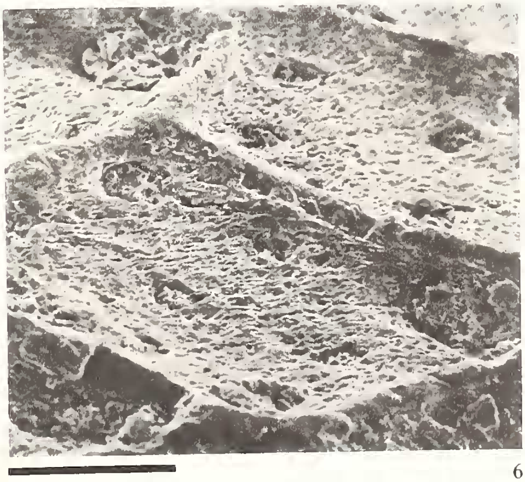
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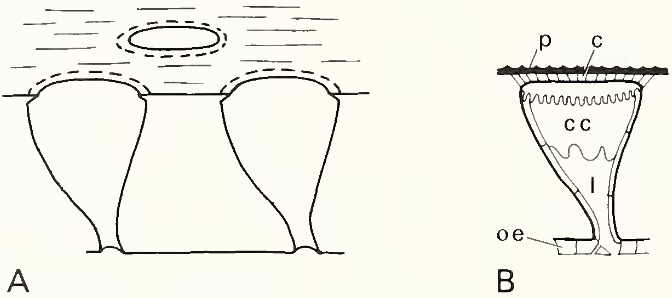
WRIGHT, *Dictyonella*

sculpture in the *Dalmanella* species, this ornament is simply a reflection of the fine concentric deposition of shell ridges produced by regular pulsatory undulations of the mantle edge between secretion of concentric sets of caeca.

Sarganostega. The spiriferinacean *Sarganostega* possesses a distinctive surface again resulting from shell punctation. Apart from radial plications, the otherwise smooth surface is pitted with coarse punctations the diameter of which on the exterior ranges from 0·02 to over 0·2 mm. The apertures are largest in the intercostal spaces, less coarse on the plications, and with progressively smaller openings in the later growth stages (Pl. 66, fig. 10). Internally the puncta are reduced in diameter through the shell to between 0·02 and 0·07 mm on the interior (Pl. 66, fig. 9). The puncta are outwardly inclined towards the posterior (text-fig. 10) in shell material which may be about 0·35 mm thick.

The specimens studied from West Texas by Cooper and Grant (1976, p. 2744) are entirely silicified, and it is noteworthy that the external apertures of the puncta commonly show a thin selvage of replaced shell material protruding from the margins, so that the maximum diameter of a punctum is situated below the shell surface. The implication is that the outer shell layer formed a continuous cover over the sites of the puncta through which the caecal brush extended in life, and despite the large size there seems little reason for regarding these structures as being more than puncta containing unusually large caeca, a modification on the function of which one can only speculate.



TEXT-FIG. 10. A—stylized longitudinal section and surface view of the *Sarganostega* shell showing the form of the puncta. Anterior to the right. B—inferred distribution of soft tissue; c—calcite canopy; cc—core cells of caecum; l—lumen; oe—outer epithelium; p—periostracum.

EXPLANATION OF PLATE 66

Figs. 1–4, 7. *Dictyonella reticulata* (Hall). Waldron Shale (Silurian), Waldron, Indiana. 1–4, longitudinal thin sections of a pedicle valve, USNM 303741. 1, anterior margin, exterior to top with pits and puncta filled with sediment, enclosed by resin, ×90; 2, detail with pits and puncta filled with sediment and pyrite (black), ×250; 3, section at posterior of valve showing colleplax separated from overlying shell by sediment, ×250; 4, section through valve showing tubular form of puncta within the inner shell, ×250; 7, cellulose peel through colleplax (lower middle of picture) showing punctation on internal (lower) surface adjacent to sediment (dark), USNM 303741, ×250.

Fig. 5. *Rhipidomella hessensis* King. Skinner Ranch Formation (Permian), Hess Canyon, W. Texas. Brachial valve exterior showing distribution of aditicules, USNM 150354 c, ×3.

Fig. 6. *Kullervo* cf. *complectens* (Wiman). Wenallt Formation (Ordovician), Garth, Powys. Latex cast of brachial valve exterior, BB 94682, ×4.

Fig. 8. *Kullervo lacunata* Öpik. Kukruse Stage (Ordovician), Kukruse (Baron Toll's estate), Estonia. Development of aditicules on geniculation at anterior of brachial valve, USNM 303726, ×15.

Figs. 9, 10. *Sarganostega pressa* Cooper and Grant. Bell Canyon Formation (Permian), Hegler, W. Texas. Interior and exterior surfaces of brachial valve, USNM 154636 b, ×6.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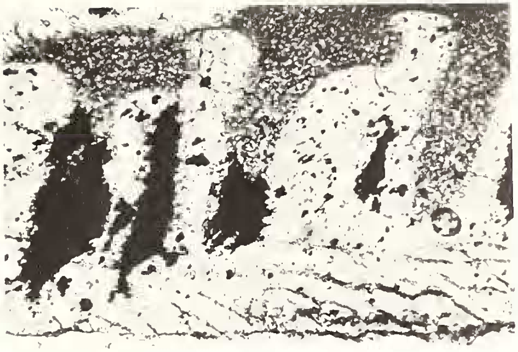
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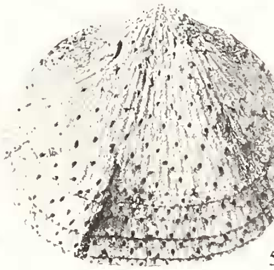
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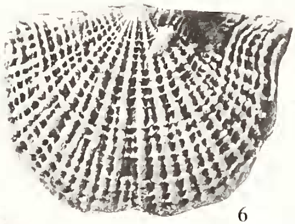
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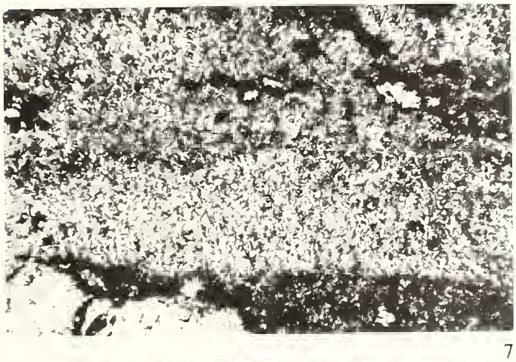
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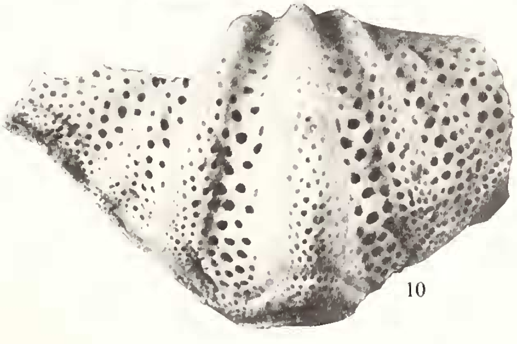
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WRIGHT, pitted brachiopods

Linoporella. This genus is characterized by rows of pits radiating from the umbo and located in the spaces between the radial ribs, so that only a single row of pits separates the adjacent ribs. As the shell grows, these ribs become broader until at a certain width a new row of pits develops more or less in the middle to divide the rib into two, a process which maintains a relatively constant pit density around the mantle edge at any one time. In addition to the pits, the shell surface shows well-marked concentric growth stages and finer growth lines traceable both across the ribs and in the intercostal spaces where they appear to separate the successive pits. This, however, is not always the case, for a growth ridge marking the front of a pit in one row may be traced across the rib to enter the next intercostal space at the middle of a pit (Pl. 69, fig. 3). This demonstrates that the pitted appearance is not produced simply by the reticulation of the intercostal spaces by well-formed growth ridges. The length of the rounded to elliptical pits varies from about 0·1 to 0·2 mm in the specimens of *L. punctata* (de Verneuil) examined and different sizes of pit in adjacent rows produce an offset pattern when, for example, four pits in one row correspond to three pits of the neighbouring row between successive growth stages.

The pits in *Linoporella* appear to be entirely a surface phenomenon and not related to shell punctation, which occurs on a very fine scale with puncta of a diameter of about 0·01 mm. An abraded shell shows that the otherwise dense and uniformly packed puncta are only poorly developed along narrow bands of shell which mark the central position of the intercostal space.

Rhipidomella. Among the punctate orthides, the surfaces of *Rhipidomella*, *Schizophoria*, *Orthotichia*, *Acosarina*, and other stocks are characterized by the development of exopuncta in the form of 'hollow costellae', a feature which occurs also in impunctate stocks. Exopuncta were defined by Schuchert and Cooper (1932, p. 10) as punctations which indent the external surface but do not pass through to the interior. Williams and Rowell noted that these superficial perforations could arise in a number of ways (1965, p. H68), and regarded the hollow ribs as being produced by a retardation of the mantle edge along the line of the rib followed by an internal sagging of the mantle as it readvances before rising to continue secreting the rib. This interpretation accounts for the basic appearance of the ribs, and that the ribs are not hollow along their length but only periodically so.

The distribution of the openings of the hollow costellae is well seen along with the much finer endopunctation in *Rhipidomella hessensis* King (Pl. 67, fig. 6). The width of the rib openings are up to about 0·2 mm, the linear density of the endopuncta is about 15 per mm. In contrast to the pitting so far discussed, the important feature of that resulting from the hollow costellae is that the pits, developing along the length of the rib, open in an anterior direction. This implies that their prime function must be related to the shell margin, and an examination of the commissure confirms that the apertures point forwards away from the shell (Pl. 67, fig. 7).

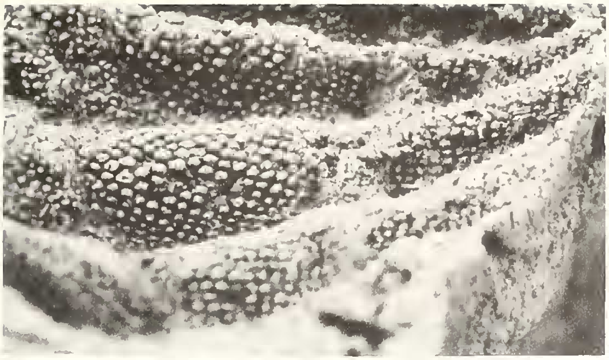
EXPLANATION OF PLATE 67

Fig. 1. *Salacorthis costellata* Williams. Spy Wood Grit (Ordovician), Rorrington, Shropshire. Detail of external mould of brachial valve, BB 37156, × 15.

Figs. 2, 8. *Saukrodictya hibernica* Wright. Dolhir Formation (Ordovician), Glyn Ceiriog, N. Wales. External mould and latex cast of brachial valve, BB 37397b, × 7.

Figs. 3, 4, 5. *Doleroides tennesseensis* Cooper. Lebanon Formation (Ordovician), Tennessee. Antero-lateral, ventral and anterior views of conjoined valves showing distribution of aditicules, USNM 110635 h, × 3.

Figs. 6, 7, 9. *Rhipidomella hessensis* King. 6, 9, Skinner Ranch Formation (Permian), Hess Canyon; 7, Bone Spring Formation (Permian), Victoria Canyon, W. Texas. 6, detail of shell surface of specimen figured in Plate 5, fig. 5, USNM 150354 c, × 15; 7, view of front margin of brachial valve showing orientation of aditicules, USNM 153775 j, × 15; 9, internal margin of brachial valve showing stages in modification of follicular embayments into setal-bearing aditicules, USNM 173756 d, × 15.



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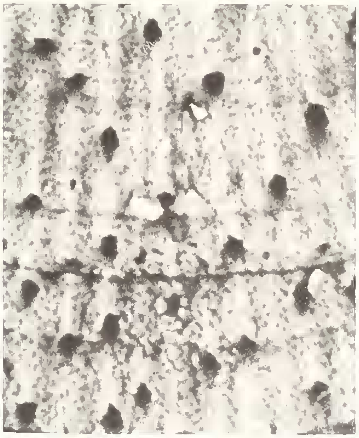

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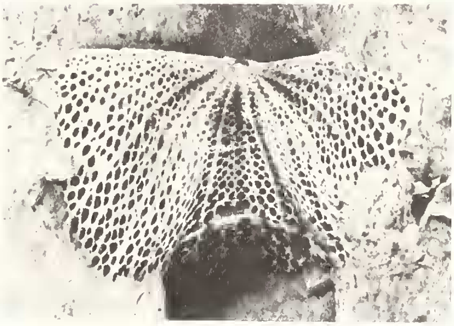

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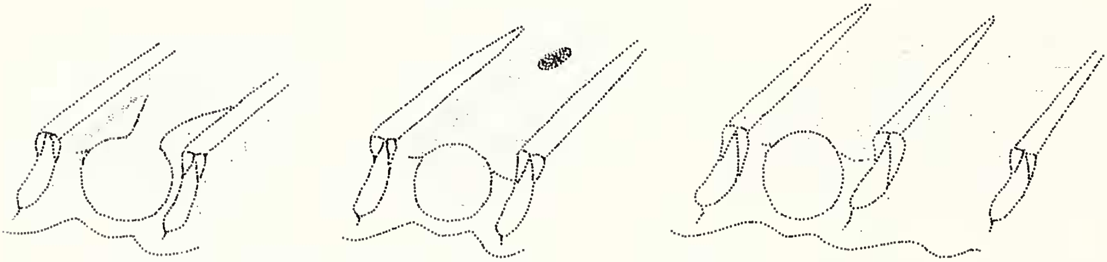
WRIGHT, pitted brachiopods

Internally the valves show well-developed marginal crenulations. The embayments of the crenulated margin of the shell in dalmanellids have been regarded by Williams and Wright (1963, p. 19) as a likely site for the accommodation of setal follicles, on the basis of the association of setal follicles with the rib embayments in extant *Terebratulina.* The situation seen in the hollow costellae of *Rhipidomella* is here interpreted as a modification of this arrangement in which setae developing along the mantle edge become sealed off along the line of the rib and replaced by new setae as the shell grows. The setae are considered then to develop along the follicular embayments as in *Terebratulina*, with the outer epithelium behind the mantle edge moving laterally around the internal edges of the setal follicle from the sides of the follicular eminences, gradually to seal off the setae within the substance of the shell. Successive phases of this development may be seen around the inner margin of the valves (Pl. 67, fig. 9), with thin selvages of shell first extending laterally from the sides of the eminences towards the centre of the embayment; then coalescing to leave an opening at the posterior maintaining contact between the setae and the mantle, before this is reduced in size and eventually sealed off to leave simply a swelling along the embayment before deposition of secondary shell masks the inner surface topography behind the advancing shell margin (text-fig. 11). The eminences and embayments are not developed postero-laterally in *R. hessensis*; on this part of the internal margin Cooper and Grant (1976, pl. 666) record ‘small borings’ and ‘tubular borings’ for the specimen shown as their figure 27 and enlarged in figure 29. The feature may, however, be observed in this position on many reasonably preserved brachial valves (Pl. 69, fig. 5) and my interpretation is that these tubes again represent the calcareous sheaths of outwardly directed setae corresponding to those of the crenulate part of the margin, and are not a result of boring by marine organisms.



TEXT-FIG. 11. Diagram showing the stages in the sealing of a follicular embayment into the substance of the shell as seen along the internal margins of *Rhipidomella hessensis* King.

The setal-bearing pits are fairly densely distributed across the brachial valve of *R. hessensis*, and near the front margin appear in successive waves (Pl. 66, fig. 5). But on the pedicle valve they are not only much less common but are essentially confined to the flanks and are lacking in the median sulcus (Cooper and Grant 1976, pl. 667, fig. 40). Thus although setae would have been present on the lateral margins of both valves, they were only developed at the front on the brachial valve of this species. The presence of setae sited on the margins of each valve would suggest that in addition to their sensory function, the setae may have had the ancillary function of screening the margin to prevent particles of too large a size from entering the mantle cavity when feeding, in a manner similar to that envisaged for the protective grille of calcareous spines at the periphery of *Acanthothiris* and other spinose shells by Rudwick (1965, p. 612) or that developed by the setae in some modern brachiopods (Rudwick 1970, p. 105) which are not emplaced in the calcareous shell. But although it is possible to envisage such a grille-like function for lateral inhalant currents it is difficult to interpret an effective screening system for the single row of setae medianly, unless the brachial valve were invariably orientated uppermost, which seems unlikely for a brachiopod with the general shape of *Rhipidomella.*

PITTED SURFACES OF IMPUNCTATE ARTICULATE BRACHIOPODS

Among the impunctate articulate brachiopods several stocks, particularly of Lower Palaeozoic age, possess a combination of both well-developed radial and concentric ornamentation. The resulting reticulate pattern has a superficial resemblance to pitting, and good examples may be found in the gonambonitacean genera *Lacunarites* and *Kullervo* (Pl. 66, fig. 6).

Pitted surfaces of the kind currently under consideration occur in the rhynchonellide *Porostictia*, several porambonitaceans (including *Porambonites* itself), and the orthide *Salacorthis*. Pits, in the form of exopuncta and hollow costellae already noted for the punctate orthides, are again not uncommon amongst the impunctate orthides and are well displayed by forms like *Doleroides* and *Plectorthis*, while the species *Kullervo lacunata* Öpik possesses anteriorly directed exopuncta along with the reticulate ornamentation (Pl. 66, fig. 8).

Porostictia. The type species of *Porostictia*, *P. perchaensis* (Stainbrook), from the Devonian of New Mexico, shows radial rows of fine pits similar at first sight to those of *Linoporella* or *Porambonites*. As indicated by Cooper (1955, p. 62), these rows of pits are separated by 'fine radial lines' which are of low relief being only slightly raised or even flat areas of shell as may be seen from the growth lines in Plate 69, fig. 6. In *Porostictia* the pits themselves are not in the typical form of a median depression surrounded by a low positive ridge of calcite, for while the posterior wall is well-defined and steep there is no corresponding anterior wall and the depression returns gently back to the normal surface of the shell exterior. The lack of definition of a front margin, making the pits incomplete, may give a scalloped appearance to the shell surface. The width of the pits is typically about 0·075 mm, but may reach 0·1 mm; the width across the areas separating the pits of adjacent rows varies from about 0·1 to 0·2 mm. The pits lie only roughly parallel to the shell margin, any such symmetrical arrangement being disturbed as a new row of pits is intercalated between two existing rows, which are moving apart radially as the shell grows. The new pit arises to occupy the position of most space between the existing pits and thus develops in quincunx with the new row appearing staggered or offset with respect to the neighbouring rows.

It should be noted that these pits occur not on the low capillae but in the spaces between, so that their development would appear unlikely to be connected with the sensory setae. With the scalloped development and absence of definition of the pit anteriorly, it is difficult to envisage a containment of epithelium budded off the mantle edge within the pit as suggested by Williams and Rowell (1965, p. H69). It may be that the cells at the mantle edge in between the low capillae have periodically secreted organic material beneath the periostracum instead of primary shell. This would account for the abrupt break posteriorly and, if their cells were gradually replaced by the standard primary shell secreting cells again at the mantle edge, the smooth anterior gradient. Such a postulated absence of primary shell from the posterior of the pit has not been verified; although a large quantity of the Percha material is available in the U.S. National Museum it is badly exfoliated and indeed, apart from the type lot, the pits themselves are seldom preserved. These pits are not the lacunae of a reticulate ornament; some organic secretion developing at the mantle edge occupied them and must have been separated from the outer epithelium immediately after this stage. Interpretation of the function of such shallow superficial pitting is very speculative, and is commented on below.

Porambonites and *Punctolira*. *Porambonites* again has superficial depressions on the shell arranged radially in single rows and separated by variably accentuated radial ribs. *P.*? *umbonatus* Cooper from Nevada has been examined, and several species from the Baltic, where the stock is best developed. The radial lines of pits again show offsetting of adjacent rows as new rows are intercalated; widths of the pits noted varied from 0·06 to 0·1 mm; a radial density of seven pits per mm was noted on the figured specimen of the porambonitid *Equirostra baueri* (Noetling) (Pl. 70, fig. 4). Despite silicification, it seems quite clear that the pits are shallow circular depressions well defined both anteriorly and posteriorly.

One of the specimens from the Pogonip Group of Nevada figured as *Porambonites*? sp. by Ulrich and Cooper (1938, pl. 53, fig. 27) is specifically excluded from *P.*? *umbonatus* in Cooper's later work

(1956, p. 609). This shell fragment has a pitted ornament which differs from the usual intercalated nature of the new rows of pits in *Porambonites* by having pits which themselves widen before splitting to produce two rows of pits. A second porambonitacean, *Punctolira*, is also figured (Pl. 70, fig. 3). The pitting is very similar to that of *Porambonites*, and the rows are again separated by radial ribs that are better developed in some individuals than others. The pits vary about 0·1 mm in length, again arranged in quincunx when a new row develops. However, the offset nature of the new row commonly disappears as space permits so that in addition to their radial alignment the pits may also become aligned with the margin of the valve.

Salacorthis. *Salacorthis* is distinguished from other described platystrophiinids principally by the presence of pitting on the shell surface. The pitting is described by Williams as being composed of 'densely distributed, deep exopuncta arranged quincuncially' (1974, p. 79). Although the preservation of the specimens in the type horizon of the Lower Caradoc Spy Wood Grit of Shropshire is mixed, some data on the pits have been obtained. On paratype BB 37155 of *S. costellata* Williams the surface diameter of a few well-preserved pits varies from 0·04 up to 0·06 mm at the front of a brachial valve about 10 mm long. The casts of the pits, although almost perpendicular to the shell surface, do have a slight anterior inclination at the interior end; they are up to 0·1 mm in length, and show marked tapering towards the interior. The inclination and tapering are confirmed in paratype BB 37156, a broken brachial valve where the pattern of the pitting is also well displayed (Pl. 67, fig. 1). The diameter of the pits in this valve shows a large variation from 0·02 to 0·12 mm; at approximately the 5 mm growth stage the median radial density of pits is four per 0·5 mm; anteriorly, however, the pits become smaller again with a density of six per 0·5 mm.

The general disposition, the inward tapering, and the diameter of the pits indicate a similarity to endopunctation, and although the diameter of the larger of the variable sized pits is on the large side for 'normal' puncta, it approaches the mean size found in the punctate, pitted *Saukrodictya*. This raises the question whether *Salacorthis* is endopunctate. In discussing the shell substance, Williams (1974, p. 79) cited a single poorly preserved exfoliated pedicle valve as revealing the impunctate nature of the shell. In examining the type and additional topotype material, one internal mould (BB 95291) appears to have pustules on its surface; but these may simply be a reflection of the coarse preservation of many moulds in this particular lithostratigraphic unit rather than an indication of an endopunctate shell. On the evidence as it stands then, the pits would appear to be restricted to the outer shell. Nevertheless, the depth of at least 0·1 mm suggests that they penetrated well into the secondary layer and technically have been endopuncta, certainly in the peripheral parts of the shell. Assuming that the pits housed caecal invaginations of the mantle in these marginal areas, it would appear that these subsequently atrophied following separation from the main outer epithelium as the secondary shell thickened.

EXPLANATION OF PLATE 68

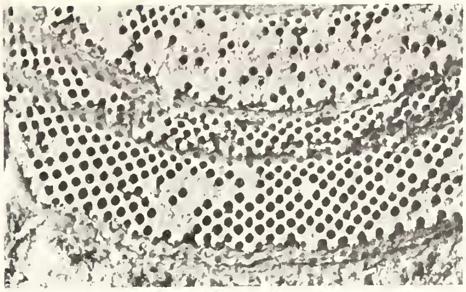
Fig. 1. *Trematis terminalis* (Emmons). Trenton Limestone (Ordovician), Trenton Falls, New York. Detail of brachial valve surface, USNM 303739, × 15.

Fig. 2. *Doleroides tennesseensis* Cooper. Lebanon Formation (Ordovician), Tennessee. Internal margin crenulations on pedicle valve, USNM 110635 f, × 15.

Figs. 3, 4, 7, 8. *Dalmanella* cf. *sculpta* Cooper. Salona Formation, Woodstock, Virginia. 3, 7, dorsal view of conjoined valves and surface detail, USNM 303736, × 3 and × 15; 4, 8, dorsal view of conjoined valves and detail of arrugiae, USNM 117364 c, × 3 and × 15.

Fig. 5. *Saukrodictya* sp. Unnamed Upper Ordovician unit USGS loc. 9166 co, Penobscot Co., Maine. External mould of damaged brachial valve showing form of pitting, USNM 188576, × 15.

Figs. 6, 9. *Dictyonina minutipuncta* Cooper. Acrothele Bed (Cambrian), Arrojos Hills, Sonora, Mexico. Exterior of valve and surface detail, USNM 116045 b, × 5 and × 15.



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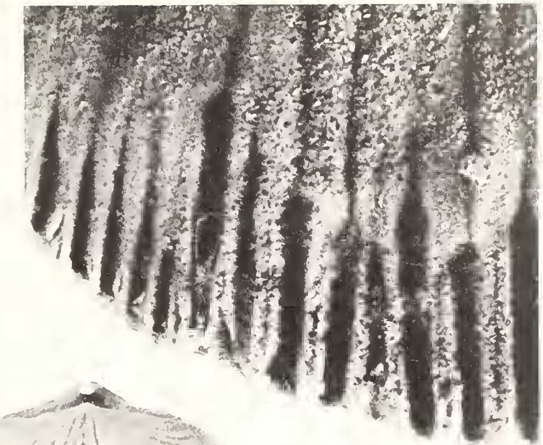

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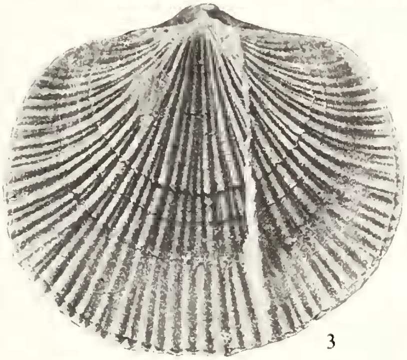

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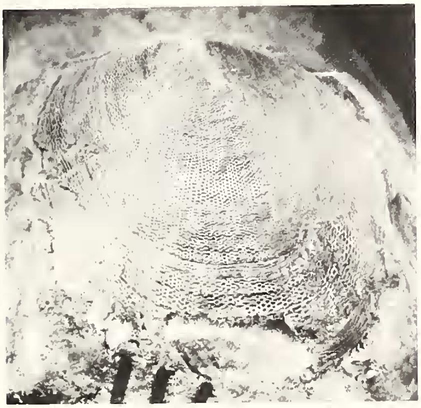

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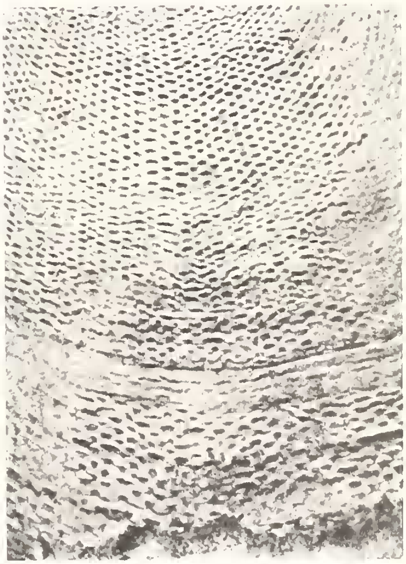


9

WRIGHT, pitted brachiopods

Doleroides and *Plectorthis*. The exopuncta of *Doleroides* in the form of hollow costellae are very similar to those described in detail for *Rhipidomella*. The deep pits lie along the length of the rib and are thus orientated anteriorly and slightly towards the opposite valve when they develop at the valve margin (Pl. 67, figs. 3-5), and are again interpreted as accommodating sensory setae along the commissure. Externally, continued shell growth results in the rib regaining its surface stature following the development of the aperture of the hollow rib. Internally, examination of the margin of *Doleroides tennesseensis* Cooper again shows well-defined swellings in the follicular embayments corresponding to the position of the hollow rib on the exterior, with a variably developed aperture at the posterior end marking the position where the setae became sealed off from the mantle and isolated in the thickening shell (Pl. 68, fig. 2). The width of the apertures on the ribs at about 0·15 mm is markedly greater than that of the openings of exopuncta with a diameter of about 0·05 mm, and which are also extensively developed on this species (Pl. 70, fig. 2). These are also located on the ribs in the form of a zigzag or staggered double row opening on either side of the rib crest and inclined obliquely forward at an angle of 50-60° to the shell surface.

The distribution of the apertures of the hollow costellae on the shell surface is uneven (Pl. 67, figs. 3-5). On the pedicle valve, a few occur scattered across the ribs of the shallow median sulcus from about the 5 mm growth stage but it is only at about 12 mm, approaching the front of an adult shell, that the apertures appear simultaneously on about half the ribs to form an arc across the sulcus; but no hollow ribs occur on either flank of the shell. On the brachial valve, the reverse is true. Here, there are no hollow ribs on the low median fold,but the flanks show a development comparable to that of the sulcus of the pedicle valve. On the specimens on which they are visible, the smaller exopuncta tend to be most readily observed towards the front of the shell and on those parts which lack hollow costellae, although they can be seen to occur along with the hollow ribs. These finer exopuncta have not been observed along the internal margin of the isolated valves available for study, nor have they been observed in the type specimens of *Plectorthis punctata* Cooper, a form on which the exopuncta of 0·06 to 0·08 mm diameter develop a paired arrangement on the broadening ribs as space allows (Pl. 70, fig. 1). At their high inclination to the surface, these pits must have opened on to the shell interior within the thin shell at the periphery of the valve. Such openings have been described from mould material of *Plectorthis* sp. by Neuman (1977, p. 21), who goes on to make the point that although the pits are exopuncta in the body of the shell, around the margin they pass through the thin shell to form endopuncta. But whether they functioned as endopuncta is a different matter.

Orthide exopuncta. It is clear, particularly from the situation in *Doleroides*, that some clarification is necessary of the commonly occurring exopuncta of the orthides. Williams and Rowell (1965, p. H68) noted that the superficial perforations known as exopuncta may have arisen in a number of ways.

EXPLANATION OF PLATE 69

Fig. 1. '*Dalmanella* cf. *sculpta* Cooper'. Rawtheyan siltstones (Ordovician), Garth, Powys. Latex cast of brachial valve exterior, BB 94674, × 15.

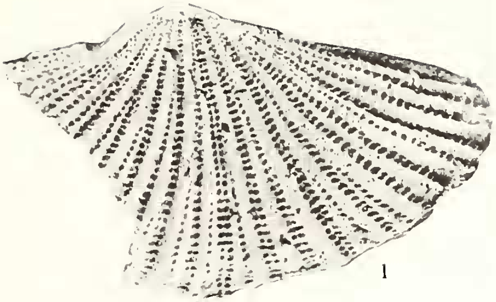
Figs. 2, 4. *Fascifera stonensis* (Safford). Dryden Formation (Ordovician), Tennessee. Exterior of brachial valve, and detail of surface, USNM 303725, × 5 and × 15.

Fig. 3. *Linoporella punctata* (Verneuil). Silurian, S. of Visby, Gotland. Detail of surface of pedicle valve, USNM 303737, × 15.

Fig. 5. *Rhipidomella hessensis* King. Bone Spring Formation (Permian), Victoria Canyon, W. Texas. Interior of brachial valve, USNM 153775 j, × 5.

Fig. 6. *Porostictia perchaensis* (Stainbrook). Percha Formation (Devonian), New Mexico. Detail from sulcus of pedicle valve, USNM 123396 a, × 15.

Fig. 7. *Dalmanella sculpta* Cooper. Salona Formation (Ordovician), Woodstock, Virginia. Detail of surface of brachial valve photographed under liquid to show puncta in addition to arrugiae, USNM 117364 c, × 15.



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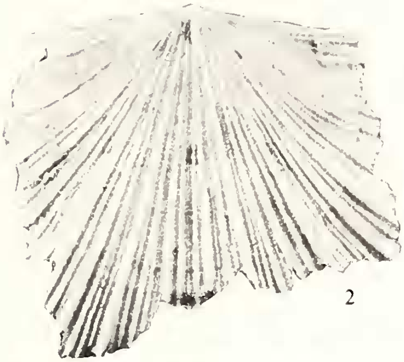

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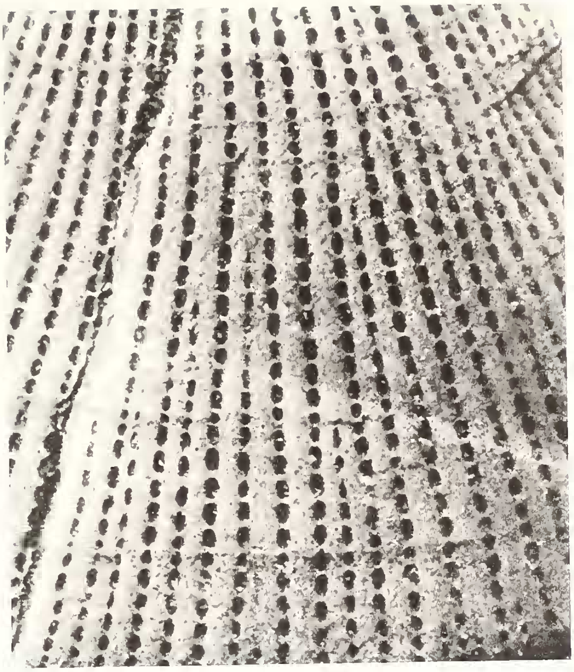

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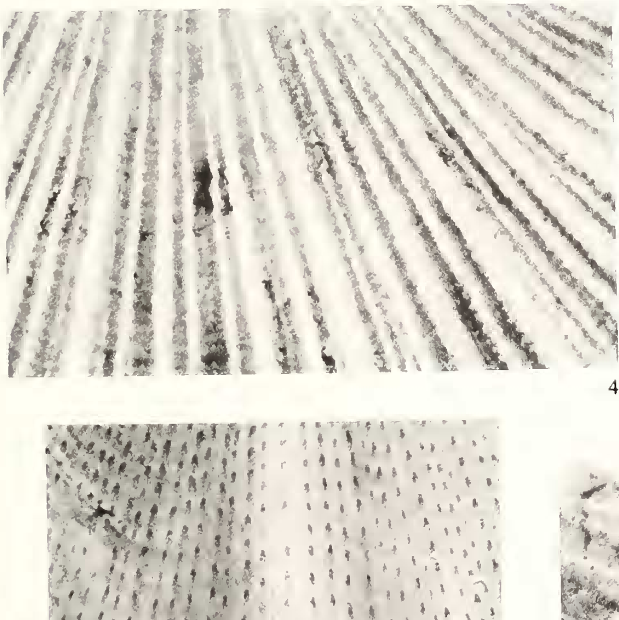

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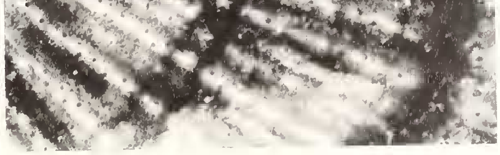

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WRIGHT, pitted brachiopods

Concomitantly, the exopuncta may also have had differing functions and although one cannot be categoric as regards the function of a feature not known in living forms, the differing size and disposition of the exopuncta do enable some distinctions to be made.

1. The exopuncta which result in the development of the so-called hollow costellae are orientated outwards from the shell margin where they are essentially in the plane of the valves; they are of relatively large size, occurring across the crest of the ribs where their continued development at the shell margin results in a series of very shallow angled perforations such as are found, for example, in *Rhipidomella*, *Schizophoria*, *Tritoechia*, and *Doleroides* and for which the term *aditicule* (latin aditiculus—small entrance, adit) is proposed. There is little doubt that these aditicules accommodated setae.

2. The very much smaller exopuncta, orientated at a steeper angle to the shell surface (with a posterior inclination from the exterior of up to about 60°) and again found on the ribs in such forms as *Plectorthis* are here termed *arrugiae* (latin arrugia—mine-shaft). These are more difficult to interpret. Williams (1974, p. 55) interprets these fine exopuncta in his species *Orthambonites exopunctata* as containing setae, but the presence of these arrugiae along with aditicules in *Doleroides* suggests that it is unlikely that both forms contained similar setae, in the sense of the marginal setae known from extant brachiopods.

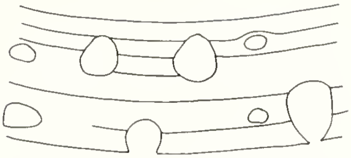
One possibility is that the arrugiae contained small bristles of a sensory nature covering a wider field at the shell margin than the setae with their more restricted outward orientation along the commissure. Again, rapid severing of the connection with the outer epithelium suggests that the marginal function soon became redundant as the shell grew although the chitinous bristles were most likely retained as spines on the shell surface during the life of the animal. An alternative possibility is that these exopuncta marked the position of impersistent caecal cups developing in the outer shell layers (Williams and Rowell 1965, p. H68; Neuman 1977, p. 21). Against this interpretation of these particular exopuncta is the fact that arrugiae are developed on shells which already possess endopuncta, and there would appear to be little point in the presence of temporary caecal cups in shells already endowed with standard caeca. *Paurorthis* is known to have both endopuncta and exopuncta (arrugiae) as indicated by Öpik (1933, p. 14); the typical exopuncta are well illustrated by Cooper (1956, pl. 151, fig. 18). Coarse exopuncta of this type have been noted in *Dalmanella sculpta*, (Pl. 69, fig. 7), and not only is their presence considered important but also the fact that anteriorly the apertures are raised on calcareous cones (Pl. 68, fig. 8). While one could expect such structures to contain fine bristles, they would seem unlikely to function as temporary caecal containers. Accordingly the view here is that in life the arrugiae contained fine chitinous bristles but which were quite distinct from the setae contained by the aditicules.

PITTED SURFACES OF CHITINOPHOSPHATIC BRACHIOPODS

It has recently been shown by Biernat and Williams (1970) that the protegula of a number of chitinophosphatic brachiopods are characterized by a pitted surface. The brachiopods were almost entirely acrotretids, together with *Curticia* and the problematic *Eoconulus*; an acrothelid, *Orbithele*, has since been shown also to have a pitted protegulum (Henderson 1974). The origin, formation, and function of protegular pitting have been discussed by Biernat and Williams (1970), Ludvigsen (1974), and Bitter and Ludvigsen (1979). A pitted protegulum is not known to characterize any of the pitted shells discussed in the present work, for although Bitter and Ludvigsen (p. 710) refer to the pitted protegular ultrastructure of *Dictyonites perforata* Cooper as illustrated by Biernat and Williams (stated as pl. 101, actually pl. 98, fig. 2), the caption to the illustration states that it is a 'young part' of the valve and Biernat and Williams specifically state that the protegular surface of this species is not pitted (p. 499).

Dictyonites and *Dictyonina*. Although the very distinctive protegula of *Dictyonites* are not then pitted, the rest of the valves anterior and lateral to the protegula are characterized by perforations which pass through the shell. The genus is known from material etched with acid from the Pratt Ferry Limestone of Alabama and described by Cooper, who pointed out that in life it was quite unlikely that the shell was perforated through its entire substance (1956, p. 187). In some specimens, when the deep pits are viewed from the inside, the external opening is seen to be narrower due to a halo of thin shell around the aperture. This suggests that very thin shell may have extended across the aperture, a possibility supported by the evidence of growth lines which run straight into the margins of the pits

TEXT-FIG. 12. Stylized sketch of part of the anterior margin of *Dictyonites* to show the relation of growth lines to surface pits, based on the brachial valve of Plate 70, fig. 5.



without deflection (text-fig. 12). Biernat and Williams (1970, p. 499) suggested that a thickened organic pad of the inner membrane of the periostracum may have covered the aperture. On the internal surfaces of the valves, some of the Pratt Ferry shells show a patchy distribution of a thickness of shell material suggesting that there may have been restriction of the internal aperture of the pits, thus resembling the punctate *Dictyonella*. The marginal limbus of either valve is also less perforated than the main shell, and may also appear meandriniform (Pl. 70, figs. 6, 8). In the specimen shown on Plate 70, fig. 5, the diameter of the pits grades from 0·02 mm in front of the protegulum to reach 0·075 mm near the front margin; in some specimens (Pl. 70, fig. 7) the pits adjacent to the protegulum are larger than many of the succeeding ones.

The disposition of the pits of *Dictyonites* is again radial, with offsetting in adjacent rows to produce the quincuncial pattern. In later growth stages, the development of extra pits, variable pit size, and general size increase produces irregularity of this basic pattern. At the periphery of the shell, a ragged appearance results from pits being incompletely developed in places at the time of death (text-fig. 12; Pl. 70, fig. 5). A noteworthy feature of the *Dictyonites* shell is that it is very thin immediately in front of the protegulum; this thickness of about 0·025 mm increases anteriorly to 0·1 mm or more in shells around the 1 mm plus length. This is the converse of the usual brachiopod pattern in which the periphery of the shell is the thinnest and the umbonal region the thickest owing to continual deposition of secondary shell by the outer epithelium throughout the life of the animal.

In contrast to the small Ordovician *Dictyonites*, *Dictyonina*, recorded mainly from Cambrian rocks, attains quite large size (10 mm or so long) and is readily distinguished by the small pits (0·02 mm long near the umbo to 0·04 mm or more anteriorly) being clearly confined to the surface layer. The honeycomb pattern is again produced by radiating rows of pits with alternate rows offset (Pl. 68, figs. 6, 9). As the shells become larger, the pits broaden and lose their definition essentially to become undulations in the concentric growth lines. This development, particularly with the loss of the well-defined anterior boundary of the pits, produces an appearance in the pitting similar to that occurring over the entire shell of *Glyptoglossella*.

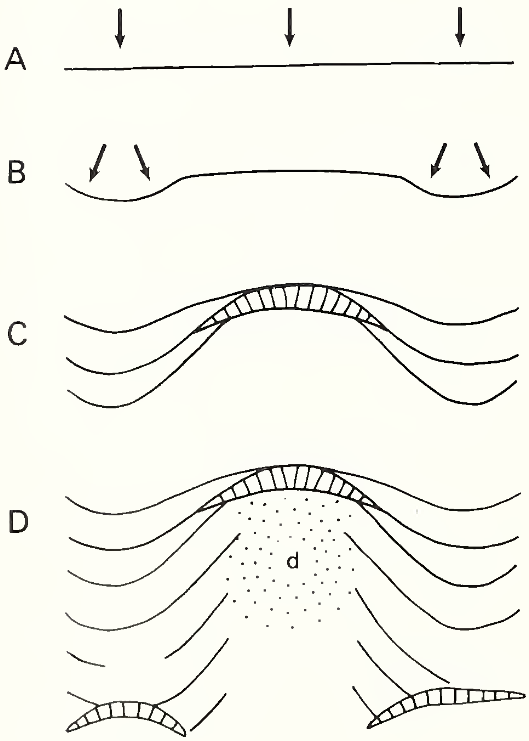
Laucunites is a third paterinid which possesses a well-developed net-like surface. This Tremadoc and Lower Ordovician form, placed closest to *Dictyonina* by Goryansky (1969, p. 103), shows a regular development of pits in offset radiating rows as discussed above. The pits were described as being relatively large and deep, and although Goryansky's figure (1969, pl. 20, fig. 10) shows them to be small in the umbonal region it also indicates that they attain a length of over 0·2 mm in later growth stages. This is very much larger than the pits of either *Dictyonites* or *Dictyonina*.

Glyptoglossella. The pore-like surface of the obolid *Glyptoglossella* Cooper is the result of the differential scalloped growth of the shell at the mantle edge, which produces a superficial appearance of pitting (Pl. 71, fig. 8). The scalloping effect is best seen on the main body of the shell, for the slower growth along the posterolateral margins of the valves results simply in fairly even and well-developed growth lines. When traced anteriorly the latter become increasingly irregular with scalloping well displayed in some specimens (Pl. 71, fig. 2).

Development of this ornamentation appears to take place in several stages (text-fig. 13). The outer epithelial cells periodically cease to grow outwards at the mantle edge over variably staggered distances each of about 0·2 mm, and in these positions shell deposition continues internally to the already deposited shell so that it thickens to produce a cliff-like edge at the posterior of the developing depression. At the same time, forward growth continues lateral to these positions, and is indicated by growth undulations in the form of a succession of anteriorly convex arcs. These spread laterally to floor the depression. The thicker median parts of the arcs along which growth has not been interrupted form the poorly defined lateral margins of the depressions while the fronts are variably defined by the posterior edge of a later depression. As in most cases the posterior of the pit forms a sharp, commonly irregular, cliff-like feature, it might be reasonably expected that some projection from the shell had been broken off; but no evidence to support this possibility has been found.

Foveola. The Lower Ordovician obolid *Foveola* has a shell surface which is densely covered with small irregular depressions, and which imparts a distinctiveness to the genus (Goryansky 1969, p. 30). From his illustrations (Pl. 3, fig. 10*a*) the pits appear to be very fine, of the order of 0·015 mm in diameter. Goryansky included within his genus specimens described by Cooper from the Pratt Ferry Limestone of Alabama as *Obolus*? sp. 4, the material of which Cooper regarded as being insufficient to establish a new genus at that time (1956, p. 193). The pits of this species have a somewhat larger diameter, between 0·02 and 0·04 mm, but a feature of the Pratt Ferry shells which is apparently lacking from the Estonian material is that although a quincuncial pattern of pits is maintained medianly, laterally, and anterolaterally, the pits become separated by ridges which trend obliquely across the shell (Cooper 1956, pl. 9, fig. 21; pl. 11, fig. 8). This development is not disimilar to that seen in the lingulellinid *Westonia*, the complications of which have been discussed already (p. 446).

Trematis. The genus *Trematis* is represented by many species which are largely characterized by the nature of the pitting on the shell surface. The pits, of variable outline, may be arranged radially as in *T. foerstei* Ulrich and Cooper (Pl. 71, fig. 7), where the shell between the rows of pits is relatively broad and flat, and as in *T. crassipuncta* Ulrich (Pl. 71, fig. 1), where the intervening shell is rather narrow, giving the aspect of radiating ribs between adjacent rows. In other species, e.g. *T. terminalis* (Emmons) (Pl. 68, fig. 1), alternate radial rows are offset to give a quincuncial pattern. The size of the pits varies over the shell and increases fairly steadily until near to the anterior margin; the last growth



TEXT-FIG. 13. Sequence of stages to show the differential growth producing the scalloped surface of *Glyptoglossella* (plan view). A—steady anterior growth; B—cessation of anterior growth medianly, arcuate growth on either flank; C—thickening of shell medianly, scalloped growth stages laterally; D—continued growth producing depression (d) in front of thickened shell.

stages are commonly marked by less than maximum size for the pits, no doubt reflecting reduced growth of the late stages. In addition to the general increase in pit diameter (from 0·045 mm for pits close to the umbo to 0·5 mm and a depth of over 0·1 mm near the front of the figured specimen of *T. crassipuncta*), the rows of pits also increase by intercalation. Pitting is not developed in the vicinity of the marginal notch of the pedicle valve.

Along well-defined growth lines the pits display varying interruption of their growth, commonly showing all gradations from a small incomplete posterior arc through to an entire pit. The evidence of growth lines across the pits (Pl. 71, fig. 6) and of well-preserved margins with depressed areas floored by thin shell show radial growth to be fairly even. Broken sections across the shell further show the outer layer which covers the crest of the defining ridges to pass down across the floor of the pit. This indicates that the surface pattern is a reflection of undulations of the mantle edge. In *T. crassipuncta* these undulations produce a succession of radially arranged depressions along narrow arcs of the mantle; in the quincuncial forms this simple pattern is complicated by the offsetting of pits in adjacent rows, so that concentric undulations of the mantle edge are also involved. Shell sections show that extra shell material is deposited, presumably fairly rapidly, internally to the initial folds of shell marking the position of inter-pit ridges. This material is absent from the thin shell of the pit which is underlain by a continuous shell lamina which shows only a modest outward deflection in the positions of the pit defining ridges. As there is no connection between these superficial pits and the shell interior in *Trematis* it would seem unlikely that the pits contained organic material other than the thin periostracal coating in the living shell, but the possibility that they contained organic secretions produced at the mantle edge cannot be ruled out.

CONCLUSIONS

1. Examination of the smooth umbonal region of *Dictyonella* indicates that the colleplax, a plate originally developing on the shell interior, is progressively exposed to the exterior by a process of resorption of the outer shell in this region; the absence of outer shell at the umbo is not a result of the shell breaking away from its position of attachment. The colleplax is considered to act as a base on which is located a chitinous pad that serves to attach the shell to the substrate.

2. The apparently complex network of variably rhombohedral to hexagonal pits on the main shell surface is considered to result from simple radial growth modified by the inevitable geometrical results of closer packing of the pits, variable rates of shell deposition over different parts of the shell, and the undulations of the mantle edge. Variation in depth of the pits appears to be a reflection of the preservation in an uncommonly spongy and cavernous shell, and when well-preserved the diamond-shaped pits may show the presence of up to nine puncta which pass through to the interior. It is considered that all the cavities within the shell contained organic material in the form of caeca, which were not simply restricted to the slender tubes penetrating the inner surface of the shell. As regards function, it seems likely that the caeca would have stored organic substances as suggested by Williams (1968*a*). Owen and Williams (1969, p. 200), in comparing samples of modern brachiopods, have noted that although the presence of punctation does not appear to affect the settling of microbenthos on the shell, it does seem to be beneficial in that punctate shells are less bored by predators, suggesting that caecal secretion inhibited penetration beneath the periostracum.

3. Despite the ready alteration of such a permeable shell as *Dictyonella*, the evidence herein of primary and of fibrous secondary shell indicates that the basic mode of shell secretion is comparable to the standard secretory regime which characterizes most orders of the articulate brachiopods (Williams 1968*b*, p. 283). If the mode of shell secretion is to be regarded as of prime importance in determining affinity among the brachiopods, this suggests that the progenitors of the Dictyonellidina should be sought among the early Ordovician Porambonitacea and Orthidina.

4. With regard to the pitted surfaces of other brachiopods, the pits are also considered to be related to the relatively large caeca in *Saukrodictya* and *Saraganostega*; in the apparently impunctate *Salacorthis* the form of the pits suggests that these also could have housed temporary caeca at the

shell margin. In *Oanduporella*, *Fascifera*, and some *Dalmanella* the fine net-like microsculpture is produced by extra calcite secretion of the cells surrounding the puncta. But in other stocks the surface pitting bears no relation to endopunctation; as such pitting is not known from extant brachiopods, interpretation must inevitably be speculative to a certain extent. Nevertheless, interpretations are suggested for the following three groups of pits which are differentiated morphologically on the basis of form and orientation to the shell surface:

(*a*) Shallow superficial pits produced by cyclic undulation of the peripheral cells of the outer epithelium and which are preserved simply as depressions in the outer shell layers. These may be arranged in radiating lines or in the various patterns which can be developed from this theme. Such pits occur both in punctate (*Linoporella*) and impunctate (*Porambonites*) stocks and while commonly of symmetrical form (*Trematis*) the anterior margin may not be defined to give a parabolic appearance in plan view (*Porostictia*); in *Glyptoglossella* the pitted appearance is the result of scalloped growth at the mantle edge. As regards interpretation, it is possible that the depressions were occupied by organic substances secreted at the mantle edge which in addition to chitinous material could have included chemical agents to inhibit the establishment of epibionts. One can further speculate that the shade (or perhaps colour) patterns so produced may have functioned as camouflage from, or mimicked warning signals to, potential predators.

While the paterinids *Dictyonina* and *Lacunites* have pits which fall into this category, those of *Dictyonites* appear to perforate the shell. Although the shells of this genus are very small (just over 1 mm), they are much larger than the protegula of acrotretids in which the pittings have been interpreted as an aid to floatation either by bubble rafting (Biernat and Williams 1970) or by structural lightening of the framework (Bitter and Ludvigsen 1979). Undoubtedly the perforated *Dictyonites* would have had a less dense shell than otherwise while at the same time the pillared nature would have been structurally stronger than an imperforate flat valve; but whether the modification was directed towards efficient floatation is uncertain.

(*b*) Relatively large, shallowly inclined aditicules developing in the ribs of impunctate (*Doleroides*) and punctate (*Rhipidomella*) orthides and which are characterized by being directed outwards from the shell margin essentially in the plane of the commissure. These are interpreted as housing marginal setae, comparable to those known in extant brachiopods except that they became embedded in the shell within a short distance of the margin. These contained setae would certainly have functioned in a sensory capacity at the shell margin, and very likely remained embedded in the outer shell throughout life. A possible additional function in some species may also have been to screen the margin from unwanted particles while the animal was feeding.

(*c*) Much smaller and more steeply inclined arrugiae, again developing along the ribs of punctate (*Paurorthis*) and impunctate (*Plectorthis*) orthides. The apertures of the arrugiae are again directed towards the commissure but at angles of about 40° to 60° with the surface. Although arrugiae may lie on the crest of the ribs in the young stages of a shell, they tend to become arranged in a zigzag pattern along alternating sides of a rib in adult growth. These directions suggest that any contained sensory bristles could act as early warning sensors scanning for approaching danger over about 100° of arc vertically about the commissure. The function of these pits, then, is also likely to have been sensory, directed towards the rapid closure of the protective valves about the attached animal.

EXPLANATION OF PLATE 70

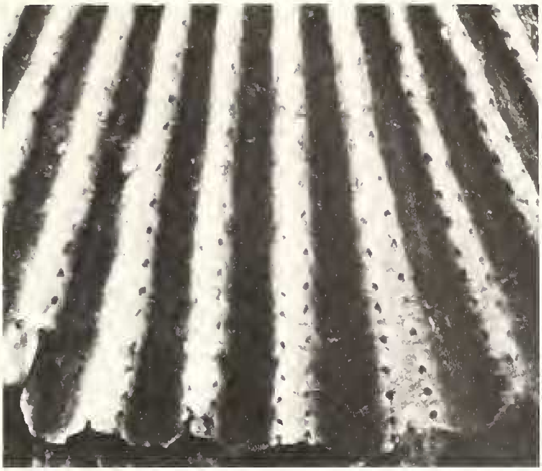
Fig. 1. *Plectorthis punctata* Cooper. Tulip Creek Formation (Ordovician), Pooleville, Oklahoma. Detail of surface of brachial valve showing arrugiae, USNM 110836 a, × 15.

Fig. 2. *Doleroides tennesseensis* Cooper. Lebanon Formation (Ordovician), Tennessee. Detail of surface of pedicle valve showing aditicules and arrugiae, USNM 110635 h, × 15.

Fig. 3. *Punctolira punctolira* Ulrich and Cooper. Pogonip Formation (Ordovician), Eureka, Nevada. Detail of exterior of brachial valve, USNM 91686 h, × 15.

Fig. 4. *Equirostra baueri* (Noetling). Jöhvi Stage (Ordovician), near Kunda, Estonia. Fragment of silicified pedicle valve showing pit pattern, USNM 303738, × 15.

Figs. 5–8. *Dictyonites perforata* Cooper. Pratt Ferry Formation (Ordovician), Alabama. 5, brachial valve exterior, USNM 116830 i; 6, pedicle valve interior, USNM 116830 d; 7, 8, exterior and interior of brachial valve, USNM 116830 k; all × 15.



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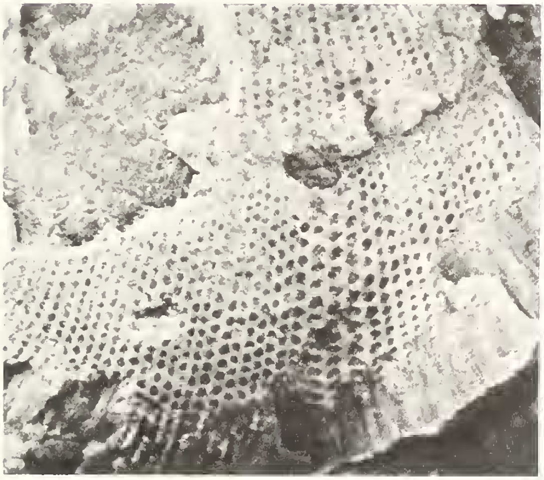

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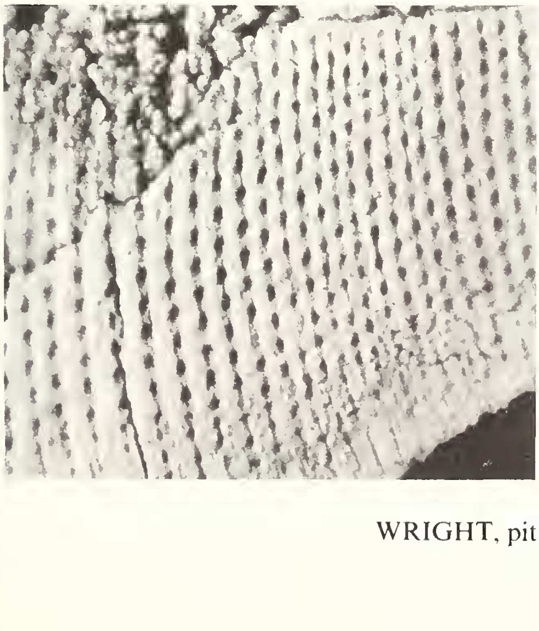

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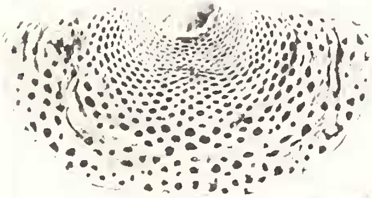

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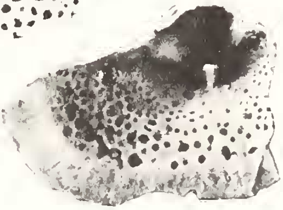

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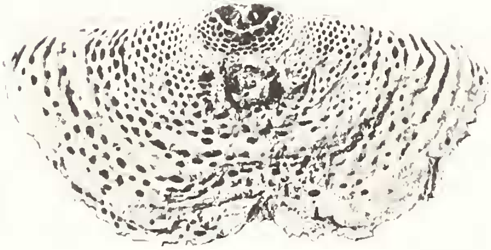

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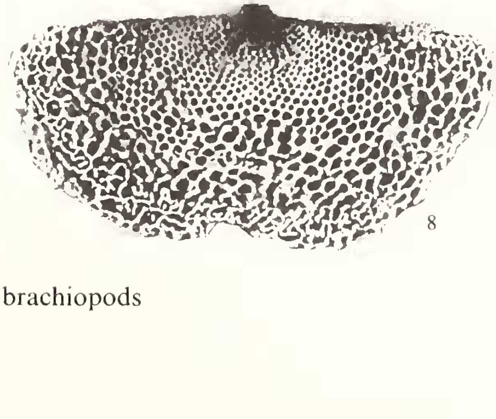


8

WRIGHT, pitted brachiopods

SYSTEMATIC PALAEONTOLOGY

Suborder DICTYONELLIDINA Cooper, 1956
Superfamily EICHWALDIACEA Schuchert, 1893
Family EICHWALDIIDAE Schuchert, 1893
Genus DICTYONELLA Hall, 1868
Dictyonella planicola sp. nov.

(Pl. 63, fig. 9; Pl. 71, figs. 3, 4, 5)

Derivatio nominis. Latin *planus*—even; *colum*—sieve, referring to the form of the surface ornament.

Horizon and locality. Boda Limestone (Ashgill), Solberga Quarry, Dalarna, Sweden.

Holotype. Brachial valve; Riksmuseum, Stockholm, No. Br 108470. Length 7·6 mm, width 10·4 mm.

Diagnosis. Dictyonella species characterized by an elliptical outline and a fine surface pitting which lacks the well-developed net-like aspect typical of the genus.

Description. Brachial valve convex, about three-quarters as long as wide and transversely elliptical in outline with almost straight postero-lateral margins diverging at about 110° from umbo; maximum valve width slightly anterior to mid-valve where curved anterior margins form obtuse angles with postero-lateral edges that turn down ventrally towards pedicle valve. Low, broad, flat-topped fold originating close to umbo, attaining width of 4·3 mm by 5 mm growth stage in *holotype* and slightly over one-half of valve width at anterior margin; anterior commissure plicate. Surface with well-marked growth stages, and well-developed pitted ornament. Over posterior of valve, shell is simply pitted, and without surface network between pits; a subdued diamond-shaped meshwork starts to develop after 5 mm growth stage. Pits near umbo very small (0·04 mm long) increasing to about 0·15 mm by 5 mm growth stage and up to 0·2 mm towards front of valve. Pedicle valve and valve interiors not known.

Remarks. Although presently represented by only a single brachial valve, the distinctive outline and style of ornamentation are considered to be sufficiently distinct from all other described stocks to justify the erection of a separate species. Until recently regarded as a typical Silurian form, the genus has been recorded from the Ordovician of Missouri and Oklahoma by Amsden (1974) but is also present, if rarely, in the Chair of Kildare Limestone in Ireland and Ashgill strata at Holmenskjaeret, Oslo Fjord, as well as in the Boda Limestone. The *Dictyonella* sp. described by Amsden, although having the finer surface pitting which would appear to characterize the Ordovician forms, differs from the new species in having a better-developed polygonal network defining the pits and also a different shell outline. The new species further differs from the American shells in having a well-developed flat dorsal fold, but it is difficult to assess the specific value of this feature from the small size of the Ordovician samples as in the more abundant Silurian species variation occurs in shape as well as in pit size as noted by Amsden (1974, p. 78).

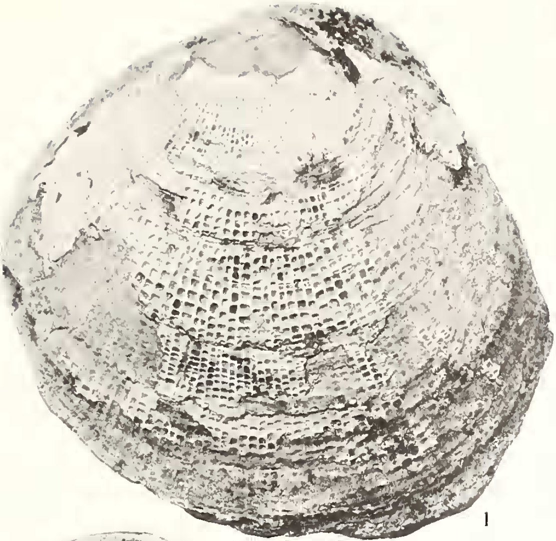
EXPLANATION OF PLATE 71

Figs. 1, 6. *Trematis crassipuncta* Ulrich. Richmond Group (Ordovician), Sterling, Illinois. Exterior of brachial valve and detail of surface, USNM 303743, × 3 and × 15.

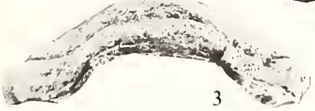
Figs. 2, 8. *Glyptoglossella cavellosa* (Cooper). Chambersburg Formation (Ordovician), Hagerstown, Maryland. 2, valve surface at anterior margin, USNM 109272 b; 8, surface of brachial valve, USNM 109272 d; both × 15.

Figs. 3, 4, 5. *Dictyonella planicola* sp. nov. Boda Limestone (Ordovician), Solberga, Dalarna. Anterior, dorsal and lateral views of brachial valve (holotype), Riksmuseum, Stockholm, Br 108470, × 4.

Fig. 7. *Trematis foerstei* Ulrich and Cooper. Plattin Formation (Ordovician), New London, Missouri. Detail of surface at front of brachial valve, USNM 303742, × 15.


1


2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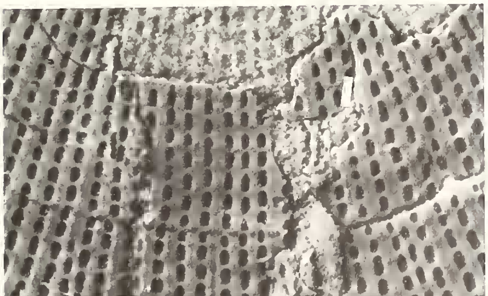
7


8

WRIGHT, pitted brachiopods

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